# Facets of the ecology, behaviour and evolution of ants

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**Facets of the Ecology, Behaviour**

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## Abstract

Three diverse aspects of the ecology, behaviour and evolution of ants were investigated.

First, a mathematical theory of combat originally developed for human warfare was applied to ants. Lanchester's linear and square laws were shown to illuminate the combat strategies in slave-making ants and army ants respectively. The equations can also be used to investigate actual conflicts and provide a valuable heuristic tool for understanding the combat strategies observed in ants.

Second, computer simulation models and analytical equations were developed to try to explain the population dynamics of the army ant *Eciton burchelli* on Barro Colorado Island, Panama. Biologically feasible predictions could be obtained even if the model colonies were assumed to jump to any patch of forest floor on the island with equal probability. A crucial parameter was found to be the probability of a patch being re-raided by a colony before that patch has recovered from a previous raid by the same colony. Seasonal reproduction and 'ancient' patches also appeared to be important.

Third, a 16 month ecological field survey of the ant *Leptothorax tuberointerruptus* was conducted on Portland Bill, Dorset. Most nests were monogynous and monoandrous. However, evidence strongly indicated that the species was also seasonally polydomous, with colonies fragmenting to occupy more than one nest site in the spring and recoalescing to a single nest site in the summer. The implications of this behaviour for the study of sex allocation are discussed.

These three topics were explored independently of one another, although they could be regarded as relating to different aspects of resource allocation in ant societies. Finally, the topics are evaluated in terms of the lessons that can be drawn for future biological studies.

## Contents

# Chapter 1

## Prologue

Three diverse aspects of ant ecology, behaviour and evolution are investigated in this thesis.

First (chapter 2), a theory originally developed to describe human warfare is applied to combat in ants, and is used principally to explain the distinct fighting strategies employed by slave-makers and army ants.

Second (chapters 3 and 4), a range of models is used to try to understand the population dynamics of a species of army ant on an island in Panama.

Third (chapter 5), a population of a species of ant on the south coast of Britain was surveyed over a period of 16 months, whereupon it was found that the colonies appear to fragment into several nest-sites in the spring and then recoalesce in the summer.

These topics were explored for their own intrinsic interest, not for their potential contribution to the understanding of one particular theme, or for the express intention of exploring a specific problem in ant biology. However, such an approach does not deny the possibility of a single theme that *is* capable of unifying the three topics, albeit in an *a posteriori* manner, and the Epilogue does indeed attempt such a synthesis.

Rather than set out from the beginning with one particular framework in mind, however, each of the topics is considered in isolation from the remaining two topics. The

reason for this was, as far as was possible, to try to avoid distortion, intentional or otherwise, of the separate topics merely so that they could be fit into an overall framework; such an exercise may have impeded the logical progress of the separate investigations in their own right. Thus each topic is addressed within a self-contained chapter complete with its own introduction and discussion or conclusions section. The three topics are presented in the order most theoretical to least theoretical, least empirical to most empirical.

# Chapter 2

# Lanchester Battles and Combat in Ants

## 2.1 Introduction

Ants of all kinds regularly engage in battles but no theory has been developed to explain or predict the outcome of such battles under different situations. This chapter shows how a series of simple equations, originally developed to describe human conflicts, can be applied to various examples of warfare in ants. Specifically, the equations prompt an explanation for the dichotomy in the fighting strategies exhibited by the two main types of ants that specialise in warfare: slave-makers and army ants (Franks and Partridge, 1993).

This chapter begins by describing the equations and the necessary conceptual framework for understanding when one type of combat might be more successful than another. The types of combat observed in slave-makers and army ants are then interpreted in the light of this framework before it is considered how the equations might be applied to, and tested against, actual battles between ants. Finally, the assumptions of Lanchester's equations are discussed and further examples of conflicts in biology which might yield to analysis by these equations are listed.

## 2.2 Lanchester's laws

Early this century, an engineer called Lanchester developed a series of coupled differential equations to describe the rates of attrition of two opposing armies at war under various combat scenarios (Lanchester, 1916; Ackroyd, 1992). Just as the original predator-prey and competition models developed by Lotka (1925) and Volterra (1926) have been considerably extended by subsequent biologists, so Lanchester's equations have engendered an enormous body of operations research (eg., Engel, 1954; Wallis, 1968; Busse, 1971; Bowen, 1973; Taylor, 1984; Adomian, 1986; Roberts and Conolly, 1992; Weale, 1992; a comprehensive overview is reportedly given by Taylor, 1983; cited in Roberts and Conolly, 1992). However, Lanchester's models have been almost totally overlooked from a biological perspective (one exception is Weiss, 1963).

Only two of the combat scenarios examined by Lanchester will be considered here. Discussion of the assumptions common to both these scenarios will be postponed until later (section 2.4.3).

### 2.2.1 Scenario 1: A parallel series of duels and Lanchester's linear law

Lanchester's linear law assumes that every individual on the minority side engages a single individual from the opposing side. Superfluous individuals on the majority side remain unengaged until enemy individuals are available for single combat. Thus the battle is comprised of a parallel series

of duels, similar to the ancient sword-and-shield type of combat in human warfare. Lanchester proposed the following pair of equations to describe the rates of attrition of the two sides:

$$\begin{aligned} dm/dt &= -\alpha\, m \\ dn/dt &= -\beta\, m \end{aligned} \qquad (m < n) \qquad \text{Eq.(2.1)}$$

$m$ and $n$ are the numbers of survivors remaining at time $t$ since the start of the battle. In this case, $m$ represents the minority side and $n$ the majority side. $\alpha$ and $\beta$ are positive constants called 'attrition coefficients': $\alpha$ represents the fighting value of a combatant on side $n$ when it is pitted against a combatant on side $m$; and $\beta$ the converse. Dividing the two equations to eliminate time and then integrating gives Lanchester's linear law:

$$\beta\,(m_0 - m) = \alpha\,(n_0 - n) \qquad \text{Eq.(2.2)}$$

$m_0$ and $n_0$ represent the numbers on sides $m$ and $n$ at the start of the battle ($t = 0$). For $m$ to win when side $n$ has been annihilated, $m > 0$. Rearranging for $m$ when $n = 0$ gives:

$$m = m_0 - (\alpha/\beta).n_0 \qquad \text{Eq.(2.3)}$$

For $m > 0$, therefore, $m_0 > (\alpha/\beta).n_0$; or $\beta.m_0 > \alpha.n_0$ (Eq. 2.4). Both sides of this last expression may be thought of as being proportional to the fighting strengths of the two respective sides in battle. If, for example, side $n$ has individuals with 16 times the fighting value of those on side $m$ (ie., $\alpha/\beta = 16$), then side $n$ only needs 1/16th as many individuals to match side $m$ in fighting strength. In other words, an army possessing combatants with massive individual fighting value stands to gain an enormous

advantage if it can ensure that the combat takes place in the form of a parallel series of duels.

Rearrangement of equation 2.3 shows that the number of casualties sustained by side $m$ when $n = 0$ is given by:

$$m_0 - m = (\alpha/\beta).n_0 \qquad \text{Eq.(2.5)}$$

Thus the number of casualties sustained by an army in a parallel series of duels does not depend on its initial numbers. The constraint of one-to-one combat ensures that greater initial numbers will not reduce the army's casualties because the number of combatants on each side fighting at any one instant can only ever be the same.

### 2.2.2 Scenario 2: Concentrated attack and Lanchester's square law

In this situation all combatants on both sides are equally vulnerable to attack from every combatant on the opposing side. Every combatant on the numerically weaker side therefore finds itself the focus of concentrated attack by more than one combatant on the opposing side. The disparity between the warring forces increases through time as the larger side brings progressively more and more of its attacking strength to bear upon the dwindling opposition. Lanchester referred to this situation as 'concentrated aimed fire', but the term 'concentrated attack' is more appropriate in a biological context. Individuals are killed at a rate proportional to the numbers on the opposing side, the constants of proportionality being the same $\alpha$ and $\beta$ as before:

$$dm/dt = -\alpha n$$
$$dn/dt = -\beta m \qquad \text{Eq.(2.6)}$$

Dividing the two equations to eliminate time and integrating gives Lanchester's square law:

$$\beta (m_0^2 - m^2) = \alpha (n_0^2 - n^2) \qquad \text{Eq.(2.7)}$$

Rearranging for $m$ when $n = 0$ gives:

$$m = \sqrt{[m_0^2 - (\alpha/\beta).n_0^2]} \qquad \text{Eq.(2.8)}$$

For $m > 0$, therefore, $m_0^2 > (\alpha/\beta).n_0^2$ ; or $\beta.m_0^2 > \alpha.n_0^2$ (Eq. 2.9). As in equation 2.4 above, both sides of equation 2.9 may be thought of as being proportional to the fighting strengths of the two sides. The square terms highlight the great importance of numbers compared to individual fighting value.

Reconsider the previous example in the case of concentrated attack. Even if combatants on side $n$ do have 16 (or $\alpha/\beta$) times more fighting value than those on side $m$, the latter need only have four times (or $\sqrt{(\alpha/\beta)}$) as many combatants to match the strength of side $n$; the individual combatants on side $m$ then last four times as long as the individual combatants on side $n$.

Unlike the linear law, the number of casualties sustained by an army does now depend, in part, on its initial numbers:

$$m_0 - m = m_0 - \sqrt{[m_0^2 - (\alpha/\beta)n_0^2]} \qquad \text{Eq.(2.10)}$$

Side $m$ will therefore sustain fewer casualties if it increases its initial numbers, $m_0$, relative to those of the enemy, $n_0$. This is because, in contrast to the linear law, attacking strength can now be concentrated.

### 2.2.3 Lanchester's square law and the power of the divide-and-conquer strategy

If a force can concentrate its attack (and the square law is therefore applicable) then it can reduce its casualties still further by employing the powerful strategy of divide-and-conquer. This is because the total fighting strength of a divided army falls below that of the intact army. Thus, the fighting strength of an army consisting of $(p + q)$ combatants may be represented as $(p + q)^2 = p^2 + q^2 + 2pq$, whereas the combined fighting strength of the two separate armies, consisting of $p$ combatants and $q$ combatants respectively, is only $p^2 + q^2$. The difference between the two quantities, $2pq$, is maximised when $p = q$; ie., when the original army has been split into two equal halves.

Consider a hypothetical engagement between 1000 predatory ants and 1000 prey ants each having equal per capita fighting value. If both armies fight *en masse* the battle will end in a draw. If, however, all the predatory ants initially engage only half of the prey, then, applying equation 2.8, the prey would be destroyed with a loss of only about 134 predators, leaving 866 to engage the remaining 500 prey in a decisive victory. This way the predators would win and still have about 707 survivors.

Consider the general situation in which side $m$ splits up side $n$ into $k$ sets of $n_0/k$ combatants each, and then takes on each set in turn with an undivided army. It can be shown (see Appendix 1) that, when $n = 0$, side $m$ will have the following number of survivors:

$$m = \sqrt{[m_0^2 - (\alpha.n_0^2)/(\beta.k)]} \qquad \text{Eq.(2.11)}$$

For $m$ to win (ie., $m > 0$), therefore, $m_0^2 > (\alpha.n_0^2)/(\beta.k)$, or $\beta m_0^2 > \alpha.n_0^2/k$ (Eq. 2.12). Comparison with equation 2.9 reveals the power of the divide-and-conquer strategy: now the fighting strength of side $m$ only has to exceed one $k^{th}$ of the fighting strength of side $n$. Obviously, the more side $m$ divides up side $n$, the bigger $k$ is, and the fewer casualties side $m$ will suffer. In the ultimate case, $k = n_0$, and $m$ therefore suffers only $\sqrt{[m_0^2 - (\alpha./\beta)n_0]}$ casualties (note the absence of the square term for $n_0$). Returning to the last numerical example, such a strategy would mean that side $m$ could annihilate the other side and suffer less than one casualty in the process ($m = 999.5$)!

I therefore predict that where (a), combat is an important selection pressure, and (b), concentrated attack closely approximates the nature of the combat (as in army ants for example; see below), then the most effective armies will employ the divide-and-conquer strategy.

## 2.3 Applying Lanchester's theories to the evolution of combat in slave-makers and army ants

For two groups of ants - slave-makers and army ants - fighting is an inevitable part of the colony's life. Both slave-makers (Alloway, 1980; Hölldobler and Wilson, 1990:448) and army ants (Gotwald, 1982; Bolton, 1990) are polyphyletic assemblages. Lanchester's theory predicts both the convergence within each of these groups and the divergence between these groups in battle strategies. The

combat strategies exhibited by slave-makers and army-ants can be neatly explained by Lanchester's linear and square laws respectively.

### 2.3.1 Slave-makers

Slave-making ants periodically attack other colonies of ants and steal their brood. The captured brood (usually only pupae) are brought back to the slave-makers' nest where they are allowed to develop into adults. These adult workers then act as slaves, performing the same routine tasks they would have done had they emerged normally in their parental nest (eg., foraging, brood care and nest maintenance).

Intraspecific slavery does occur in ants (eg., see Hölldobler, 1976; Stuart and Alloway, 1983), but more work has been done on interspecific slavery, which appears to have evolved independently at least ten times (Franks and Bourke, 1988). In a rule named after him, Emery (1909) noted that social parasites in ants, including slave-makers, were always similar to, and presumably closely related to the host species that they parasitize. No reliable case of one species of ant enslaving another that belongs to a different taxonomic tribe has ever been documented (Hölldobler and Wilson, 1990:464).

The more advanced slave-maker species, in terms of their dependency on slaves for long-term survival and productivity of the colony, can barely survive in the absence of their slaves (Stuart and Alloway, 1985). For example, workers of the obligate slave-maker, *Leptothorax*

*duloticus*, are normally nourished by food regurgitated by their slaves, *L. curvispinosus*; and colonies that have been experimentally deprived of their slaves deteriorate rapidly (Wilson, 1975). Thus many slave-maker species, the obligate slavers in particular, are trophically dependent on their slaves (Franks *et al.*, 1990). The phylogenetic affinity of slave-makers to their slaves (Emery, 1909; Franks and Bourke, 1988) presumably means that slave-makers are not any more efficient at utilising energy than their slaves. These energetic constraints mean that slave-maker workers are often outnumbered by the workers in the colonies that they raid for brood (Hölldobler and Wilson, 1990:462).

Since slave-makers do not have the luxury of numerical superiority then, unless they employed the divide-and-conquer strategy, they could not use the square law method of concentrating their attack to gain any advantage. Indeed, the slave-makers must prevent the defending host workers from concentrating their defences and using the strategy of the square law against them. Instead, the slave-makers are much more likely to win in conflicts against the defenders if they engage only one at a time, a situation described by the linear law. Section 2.2.1 showed that such conflicts are most likely to be won by the slave-makers if they have superior individual fighting value.

This prediction is unequivocally supported: slave-makers are typically larger and better adapted for fighting than the defending workers of their host species (Hölldobler and Wilson, 1990:454-463; see also Buschinger *et al.*, 1980,

for a general review of slave-maker fighting techniques). Not only are slave-makers heavily armoured and equipped with savage mandibles (eg., *Polyergus rufescens* and *Strongylognathus alpinus*; Hölldobler and Wilson, 1990:463), or deadly stings (eg., *Leptothorax duloticus*, *Epimyrma ravouxi* (= *goesswaldi*) and *Chalepoxenus* species; Buschinger *et al.*, 1980), but it is also very common for them to use so-called 'propaganda substances'. In some species, *Formica pergandei* and *F. subintegra* for example, these chemicals are simply the alarm pheromones of the defending species, thereby causing the defenders to scatter in disarray (Regnier and Wilson, 1971). In others, such as *Harpagoxenus sublaevis*, they actually cause defending workers to attack one another and form scrimmages of struggling bodies (Allies *et al.*, 1986). In the latter case, such slave-makers are apparently, therefore, using the defending colony's superior numbers to their own advantage: the defenders are effectively employing the square law and concentrating their attack in upon themselves. Any scattered defenders that are not absorbed into struggles with their nestmates can be disabled or killed with ease by the well-equipped slave-makers on a one-to-one basis. Certain species of slave-maker also lead some of their slaves into battle, thereby boosting their own numbers (Alloway, 1979).

The weapons at the disposal of the slave-maker workers are also possessed by the slave-maker queen. To found a new colony of slave-makers she first has to fight her way alone into the nest of a host species to kill its queen and

subjugate or drive off its workers (see Hölldobler and Wilson, 1990:455-458 for examples).

Finally, I could find no reports in the literature of slave-makers employing the divide-and-conquer strategy in the sense of section 2.2.3, namely the concentration of attack by a group of slave-makers on a numerically inferior subset of the defending hosts. However, descriptions of fighting are usually qualitative and do not report the details of the numbers engaged in particular conflicts. It therefore remains open as to what extent slave-makers employ the divide-and-conquer strategy.

### 2.3.2 Army ants

Army ants may be defined behaviourally as nomadic group predators (Wilson, 1958) and, as such, they are found in several subfamilies of ants, most notably the Dorylinae and the Ecitoninae. All army ants have relatively large colonies, boasting hundreds of thousands, or even millions, of workers (Schneirla, 1971:23) that can be simultaneously deployed in attacking their prey, typically large arthropods and the adults and brood of other social insects. At the very least, the army ant syndrome has evolved twice (see Gotwald, 1982, and Bolton, 1990).

One of the most intensively studied army ants is the neotropical species *Eciton burchelli* (eg., Rettenmeyer, 1963a; Schneirla, 1971; and Franks, 1982a, 1989; see also chapters 3 and 4). Hundreds, or even thousands, of the workers in an *E. burchelli* colony may die every day in the

course of combat with their prey, which primarily consist of other social insect colonies (ants and wasps mainly) and large arthropods such as crickets, cockroaches and scorpions (Rettenmeyer, 1963a:355-356, 360; Franks, 1982a). Relative to individual army ant workers these prey, including the workers of the prey ant colonies, are large and dangerous (N.R. Franks, pers. comm.) and can therefore only be overwhelmed by the concerted action of the army ants. Large prey individuals are surrounded, pinned down and then torn apart by the army ants grabbing their extremities and pulling in opposite directions (Dumpert, 1981:241). In other words, by virtue of their relatively small size, the army ants are able to exploit their superior numbers to the full by concentrating their combined fighting value on individual prey. Lanchester's square law therefore suggests itself as the ideal candidate for providing accurate quantitative predictions of the dynamics and outcome of battles between army ants and their prey.

The square law implies that even small numerical advantages can reap disproportionately large combat benefits. So why then, if the square law *is* applicable in this case, do army ants appear to overwhelm their enemies by at least one order of magnitude? Why do army ants have tens of thousands of workers per square metre at the swarm front (N.R. Franks, pers. comm.) whereas prey colonies only number from a few hundred to a few thousand? The reason is that winning a battle is not sufficient for army ants to survive, casualties must also be minimised as far as possible.

For instance, a colony of *E. burchelli* will start to dwindle in size if even only 1 to 2% of the foragers are lost on every raid. This estimate was calculated as follows. An average *E. burchelli* colony produces about 55,000 new workers (Franks, 1982a) in every 35 day activity cycle and also sends out foraging raids on 27 of the days (ie., on 13 days of the statary phase and on all 14 days of the nomadic phase; see section 3.1.2b of chapter 3). Thus, if the colony is not to grow in size, 55000/27 = 2037 workers must be killed or lost in each of the 27 raids. Since the largest of these raids has 200,000 ants (Willis, 1967), then 2037 workers amounts to at least (2037/200000) x 100 ≈ 1% of the daily foragers.

Army ants appear to be well adapted for concentrating their attack. Most army ant workers have degenerate vision (Schneirla, 1971:27-29) and therefore may encounter a prey colony at any point along the raid front with probably little warning in advance. However, their poor visual acuity may be an asset in maintaining colony cohesiveness, since army ants apparently rely heavily on short range tactile and chemical communication in maintaining contact with their nestmates (see also Franks and Partridge, in press). Together, the tendency of army ants to remain in close proximity to each other, and the efficiency of their trail pheromone recruitment system (Chadab and Rettenmeyer, 1975), mean that large numbers of workers can be rapidly funnelled into any battle-site at the front (Franks, Gomez, Goss and Deneubourg, 1991). By concentrating their attack

in this way, army ants are likely to minimize their casualties by dividing and conquering each nest the instant it is detected.

*E. burchelli* has four morphological castes of workers and the two smallest castes account for 97% of all the ants at the raid front (minims: 22%, and mediums: 75%; Franks, 1985). Lanchester's square law offers the best explanation for this high percentage: numbers are more important than individual fighting value for concentrated attack. Small workers can also be produced faster than larger workers. The importance of numbers also helps to explain why army ant colonies reproduce by fission and why the queens have such prodigious fecundity (Rettenmeyer, 1963a:370; Schneirla, 1971:126): large colony size must be maintained during the entire life-cycle if army ants are to survive.

## 2.4 Testing Lanchester's laws on actual battles

### 2.4.1 Possible candidates for testing Lanchester's laws in the context of intraspecific battles

Many ants fight members of their own species, especially in the context of territoriality or when competing for access to food. For example, workers from one nest of the wood ant *Formica polyctena* will engage in territorial battles with workers from a neighbouring nest, particularly when demand for food exceeds supply (Mabelis, 1979). Moreover, wood ants can spray their opponents with poison from a distance (Dumpert, 1981:258). Of all the types of combat between ants this would probably allow the greatest concentration of

attack because, from a distance, a greater number are able to surround their enemy. Thus battles between wood ants might show one of the closest agreements to Lanchester's square law.

Other examples of species that engage in intraspecific territorial disputes, and which might prove amenable to analysis by Lanchester's laws, are: *Tetramorium caespitum* (Mabelis, 1979; Hölldobler and Wilson, 1990:462); African weaver ants, *Oecophylla longinoda*, and *Pogonomyrmex* harvester ants (Hölldobler and Lumsden, 1980); *Azteca trigona* (Adams, 1990); *Atta* leafcutter ants (Rockwood, 1973; cited in Adams, 1990); and *Myrmecocystus mimicus* honeypot ants (Hölldobler and Lumsden, 1980).

Even when no physical aggression occurs, as is often the case in disputes between colonies of the honeypot ant *Myrmecocystus mimicus*, the outcome of the ritualised combat appears to depend heavily on the relative strength of the opposing armies (Hölldobler, 1976; Hölldobler and Lumsden, 1980; Lumsden and Hölldobler, 1983; Hölldobler and Wilson, 1990:407; Franks and Partridge, 1993).

### 2.4.2 Estimating the attrition coefficients and determining which law is applicable: a few caveats

The relative fighting values of the two sides and which, if either, of the linear or square laws is applicable, can be deduced from data on the numbers of survivors at various times after the start of the conflict. Algebraic manipulation of Lanchester's laws reveals the following:

1) If the linear law applies then a graph of $m$ versus $n$ will be a straight line with slope $\alpha/\beta$ and intercept $(m_0 - (\alpha/\beta)n_0)$.

2) If the square law applies, however, then a graph of $m^2$ versus $n^2$ will be a straight line of slope $\alpha/\beta$ and intercept $(m_0^2 - (\alpha/\beta)n_0^2)$.

Once $\alpha$ and $\beta$ are known, their values can be used to predict the outcome of any other battles. Remember, though, that a particular value of $\alpha$, for instance, applies to the affect of species $i$ on species $j$, and is not attached to $i$ independent of the identity of its enemy.

In intraspecific conflicts $\alpha$ and $\beta$ are likely to be identical and therefore cancel out from Lanchester's equations. Further, if, in addition to $\alpha$ and $\beta$ being identical, the initial numbers are the same (ie., $m_0 = n_0$), then both equations 2.2 and 2.7 simplify to $m = n$: the predictions of the two laws are identical. Thus if intraspecific conflicts are to be analysed to determine which, if either, of the two laws are applicable, then it would be prudent to make the initial numbers on the two sides very different. This has to be weighed against any consequent technical problems in monitoring the progress of the battle, since the greater the initial disparity in the two forces the quicker the battle is likely to reach a conclusion.

Finally, $m_0$ and $n_0$ must be carefully defined. They do not necessarily refer to the size of the entire ant colonies at war; rather they refer to the actual numbers in conflict.

### 2.4.3 Assumptions common to the linear and square laws

Robinson (1979) lists six important assumptions common to Lanchester's laws. The validity of these assumptions to a particular situation must be evaluated on a case-by-case basis, but any violations may be addressed by extensions of the original equations which allow for the relaxation of one or more of the assumptions (see the next section). The six assumptions and the general validity of each to combat among ants will now be examined in turn.

1) Only two sides engage in battle. Even though an army ant colony may be simultaneously attacking more than one social insect colony, such conflicts are likely to be occurring on different parts of the raid front and could, to some extent, therefore be treated as isolated battles each involving only two sides.

2) Strategies are fixed and cannot be changed once the battle has commenced. Combat strategies in ant battles probably only change over an evolutionary timescale (see section 2.5 below), although some variation might occur within a battle.

3) Both sides commence battle at the same instant and thereafter neither side receives reinforcements nor sustains losses other than those inflicted by the opposing side. This assumption will be violated by recruitment of more nestmates to a battle or by mass disarray and retreat.

4) Any individual combatant can only exist in one of two states: fully functional or utterly destroyed. Lanchester's equations are continuous (differential)

equations which often, therefore, generate fractional results. The numbers surviving at time *t* can, however, be loosely interpreted as the 'average' numbers surviving at that time, although this approximation becomes increasingly invalid as the numbers on either side approach zero (Wallis, 1968; see also Ancker and Gafarian, 1987). Incidentally, difference equations are not appropriate because they would imply that the numbers on both sides changed only in response to events at the end of the previous discrete time-step. In reality, especially in close-quarter combat, the combatants on one side are more likely to be instantaneously and continuously reducing the numbers on the other side.

5) All combatants on the same side have identical destructive capability. This assumption is most likely to be violated in polymorphic species, such as many species of army ants (but see the next section).

6) A combatant destroys enemy combatants at a constant rate until either all the enemy combatants are destroyed or the combatant is itself destroyed. This assumption is particularly important for the square law since Lanchester assumed that there are always enough of each side remaining to ensure that every attack will be equally effective. Thus the square law will not be valid when the number of participants is small, as, for example, when the battle is fought to near annihilation (Wallis, 1968).

Two further points remain. First, Lanchester's original laws are deterministic: they do not reveal the

variation in possible outcomes or the probability of any one particular outcome. Thus although one side might win in a deterministic system, it would not win every time in a stochastic situation. To increase the certainty of a given outcome, therefore, the disparity between the two sides should be increased. This is true both for the individual fighting value and for the numbers of combatants. Second, if an army has perfect knowledge of the size and strength of its enemy then, in principle, it could calculate the exact size and strength of the forces required to achieve a desired outcome. Conversely, if the army is to face an enemy of unknown size and strength, then the army should have as much fighting strength as possible. Both these points imply that, in the absence of any constraints, an army should be as large and as strong as possible in order to increase the certainty of winning.

### 2.4.4 Relaxing the assumptions and extending the equations

Returning to assumption (5) above, Lanchester (1916) showed that his square law can be modified to apply to battles between sides separately comprising more than one type of combatant (see also Roberts and Conolly, 1992). The fighting strength of a component (group of combatants of the same type) within such a heterogeneous force is simply the fighting value of its individual combatants ($\alpha$ or $\beta$) multiplied by the square of their number. The combined fighting strength of the whole side is then proportional to the square of the sum of the square roots of the fighting

strengths of its individual components. Essentially, the central message of Lanchester's square law remains unaltered: numbers matter more than individual fighting value in a situation of concentrated attack.

Morse and Kimball (1951) extend Lanchester's original equations to take into account both recruitment and also losses for reasons other than direct combat mortality. Wallis (1968), Robinson (1979) and Ancker and Gafarian (1987) address stochasticity.

### 2.4.5 Failure of the predictions and interference by alternative selection pressures

If the predictions of the laws fail, even after taking into account various extensions of the equations, then the laws themselves may not be applicable to the particular ways the ants fight. Perhaps the ants employ a mixture of the two strategies best described by an equation with an exponent somewhere between one and two, the precise value depending on which law it is closest to. Alternatively, the possibility always remains that some ants employ a radically different type of combat strategy that cannot be adequately described by Lanchester's laws or their extensions.

Moreover, combat may not have been the driving force in the evolution of particular types of ants, such as slave-makers and army ants. Many other selection pressures may impinge upon the number and fighting value of individuals. These might include the costs of producing and rearing many large individuals as opposed to a few small individuals.

The surface area over which metabolic heat loss can occur per unit volume also increases as size decreases; thus raising the commensurate costs of producing and maintaining a unit amount of biomass. Moreover, the costs of transport (in terms of energy expended per unit weight per unit distance) increase as body size decreases (Jensen and Holm-Jensen, 1980; cited in Burton and Franks, 1985); an important consideration for highly mobile animals such as army ants (Franks, 1985; Burton and Franks, 1985; Bartholomew *et al.*, 1988). Trade-offs might therefore be expected between fighting value and numbers and other adaptations for successful reproduction and survival.

## 2.5 Arms races

Even though battle strategies may be fixed in any given battle between two sides (see assumption (2) in section 2.4.3 above), both sides have the potential to develop appropriate counter-measures over an evolutionary timescale. Thus arms races (Maynard Smith, 1982) may develop with respect to battle strategies and also to variations in numbers, individual fighting value, or both.

In general, the parasitic slave-maker ants probably win the arms race against their host species. First, presumably due to their trophic dependency on the host species, the colonies of a given species of slave-maker are usually scarce compared to those of their hosts (Buschinger *et al.*, 1980), and therefore the slave-makers are rare enemies. Second, slave-makers specialise in attacking three species

at the most (known slave-makers and their host species are listed in Table 12-1 of Hölldobler and Wilson, 1990:438) and therefore can hone their combat strategies to maximum efficiency over evolutionary time. That slave-makers have developed highly effective mechanical and chemical weapons was amply demonstrated in section 2.3.1 above.

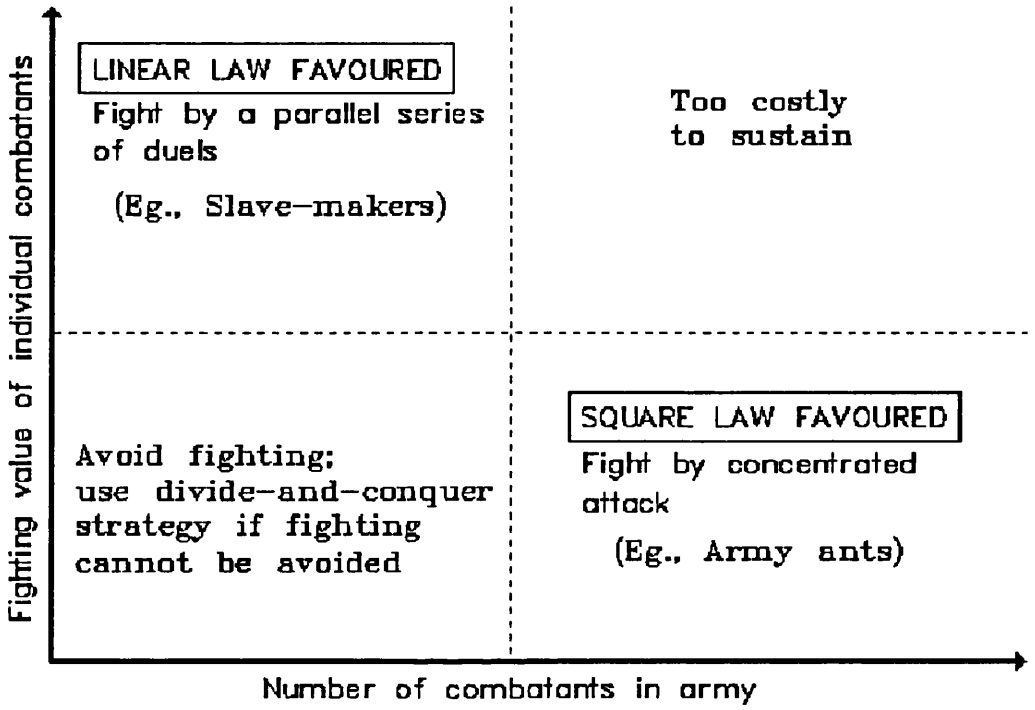
In contrast, army ants encounter a wide variety of potential prey among the diverse fauna of the tropical forest floor (although different species of army ant do appear to specialise to some degree; eg., see Rettenmeyer, 1963a, and also section 3.1.3c in the next chapter). Thus army ants can ill-afford to fine-tune their predatory techniques to one particular species, which might be widely dispersed and rarely encountered. On the other hand, and for the same reason, a given prey species might find it too costly to specialise in its defence against a rare enemy.

## 2.6 Combat space

As well as providing quantitative predictions, Lanchester's laws are heuristically valuable in providing a conceptual framework for understanding the combat strategies exhibited by ants (and other organisms; see the next section). Fig. 2.1 is a graph of individual fighting value versus number of combatants (which is related to colony size). The plane defined by these axes may be referred to as 'combat space', and a particular species could be plotted as a point somewhere in this space. More precisely, as a colony grows it may change both its size and the fighting value of its

workers, and thus describe a trajectory in combat space over time.

**Figure 2.1 'Combat space', a plane defined by the axes of combatant fighting value versus the number of combatants within an army.**




A colony or species that lies near the origin of this graph will have few workers, each with low individual fighting value, and should therefore avoid fighting. Individual workers are proportionally more valuable to small colonies and therefore should be conserved if at all possible. Should the colony be forced to fight, however, Lanchester's square law suggests that it would have to adopt a divide-and-conquer strategy to maximise its chances of survival. Note that what constitutes a 'small' or 'weak' army depends on the sizes and strengths of the other armies

surrounding it; a colony or species can only be positioned on the graph in the context of its natural competitors and enemies.

An army in the upper right portion of Fig. 2.1 would probably be too costly to sustain in evolutionary terms. This is probably why there are no species of army ants with large numbers of workers which are individually as heavily armed as slave-makers. A botanical equivalent of this would be a plant that produced large numbers of large seeds: such a plant would be unlikely because of the trade-offs that have to be made when resources are limited.

The upper left portion of combat space corresponds to species like slave-makers: few workers with high individual fighting value. Lanchester's theories suggest that such species would do best to organise their battles in the form of a parallel series of duels, as described by the linear law.

Species like army ants map to the lower right portion of the graph: lots of workers with low individual fighting value. Lanchester's theories suggest that such species would profit most by combining the efforts of their workers and concentrating their attacks on the enemy, as described by the square law.

## 2.7 Wider applications of Lanchester's laws

Lanchester's theories might be extended to other combat situations both within ants and outside ants. Within ants, the following scenarios might be usefully explored:

1) Battles between so-called 'thief' ants and the colonies of neighbouring, larger ant species from which they steal the brood for food. Examples of thief ants include *Solenopsis (Diplorhoptrum) fugax*, *Monomorium pharaonis* and species in the genus *Carebara* (Dumpert, 1981:187).

2) Colony foundation by single ant queens. A solitary queen needs to be heavily armed if, once discovered, she is to survive the attacks of workers from a large, well-established colony close to where she is founding her nest. Moreover, the first workers of a founding colony are exceptionally small ('nanitics'). One of the reasons that several small workers are produced rather than one large one might be the advantages of greater numbers when defending the colony against attack from rival colonies. Of course, an alternative explanation is that two smaller workers can perform tasks more efficiently than one large worker; or again, it might be less risky for a queen to spread her meagre resources across several workers rather than 'gambling' them on a single large individual.

3) Ants preying on termites; eg., *Megaponera foetans* preying on the termite *Macrotermes bellicosus* in Nigeria (Longhurst and Howse, 1977, 1979).

Lanchester's theories might also yield productive insights into the following examples outside the realm of ants:

1) Myxobacteria (see Franks and Partridge, in press).

2) Reactions between antibodies and antigens in the immune system. Lanchester's square law might be applicable to the

way antibodies tend to bind in clusters to their target antigens, thus concentrating their attack against the antigens.

## 2.8 Conclusions

In summary, Lanchester's laws explain battle strategies in ants as diverse as army ants and slave-makers; they may also be used to predict the dynamics and outcome of a given conflict; and, finally, they provide a useful organising principle for thinking about combat in ants. Lanchester's laws apparently represent the first theoretical framework to be applied to the analysis of direct combat between ants.

# Chapter 3

## The Population Dynamics of the Army Ant *Eciton burchelli*. I. Background and a sophisticated model.

### 3.1 Introduction

Despite the importance of social insects in terrestrial ecosystems (Wilson 1987, 1990), virtually no work has been done on their population dynamics. This chapter is the first of two that explore the population dynamics of a species of army ant on an island in the Republic of Panama.

The goal of the research was to develop a predictive and quantitative model of a tropical rain-forest population. Some of the models (particularly those in the next chapter) were designed to employ the minimum number of simple measurable parameters. The effects of varying these parameters on the population dynamics were to be predicted, particularly where those parameters had special importance from a conservation perspective; eg., island size and habitat quality.

The present chapter begins with an explanation for the selection of Barro Colorado Island (BCI) in Panama as the study site and *Eciton burchelli* as the species of army ant to be studied. After outlining the natural history of *E. burchelli* on BCI, it is then argued that the population is most likely to be regulated both by intraspecific competition for food and also by mortality inflicted by the defending social insect prey. Initially, a sophisticated simulation model was developed, using much of what is known

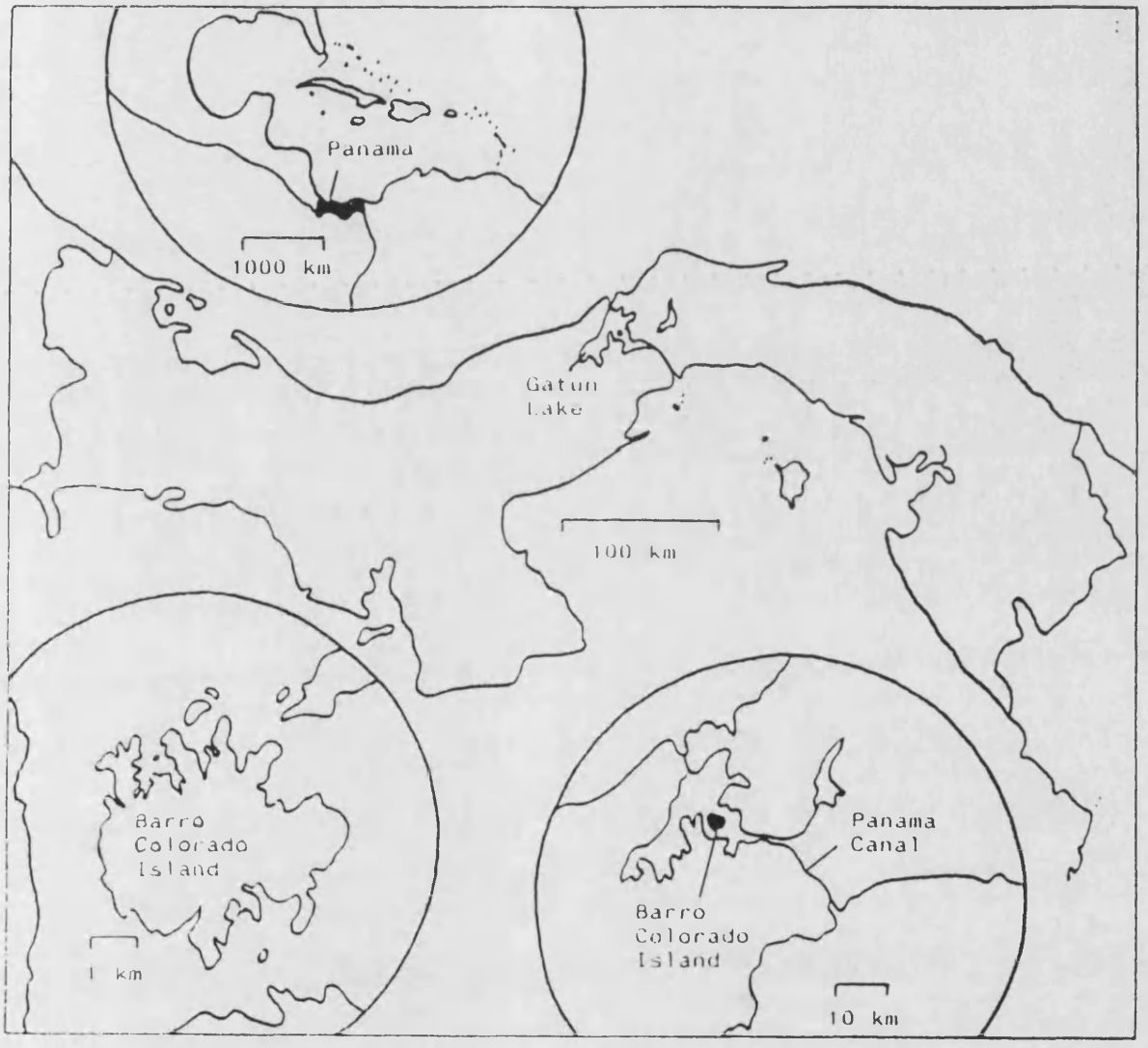
about *E. burchelli* on BCI. The model was constructed, first, to check the census estimates and, second, to provide as accurate a picture as possible of the population dynamics. This model and its main findings are described and then the problems encountered with developing and exploring such a model briefly discussed. The analysis of the complex model was intended to facilitate the isolation of the most important factors affecting the population dynamics. The effects of these factors could then, in their turn, be explored in greater detail in simpler, more abstract models. The development of these simpler models, together with the parallel construction of their analytical analogues, is described in the next chapter.

### 3.1.1 Barro Colorado Island and *Eciton burchelli*

Barro Colorado Island ($9^{o}09'N$, $79^{o}51'W$) was originally a hilltop that finally became isolated from the surrounding mainland in 1914, seven years after the Chagres River was dammed to form Gatun Lake during the construction of the Panama Canal. The vegetation of BCI is semideciduous lowland forest (Foster and Brokaw, 1982), and the island's climate is characterised by a dry season which usually starts in late December, and a rainy season which usually starts at the end of April (Rand and Rand, 1982). The location and general shape of BCI is shown in Fig. 3.1.

BCI was deemed suitable for the study of its population of *Eciton burchelli* colonies for several reasons. Since BCI is an island, any changes in the population size of *Eciton*

**Figure 3.1 Maps of Panama at various scales showing the location of Barro Colorado Island within Gatun Lake. Redrawn from Hubbell and Foster (1986).**



*burchelli* can only be due to fission, fusion, or death of the colonies rather than to emigration or immigration. Large-scale recent disturbance by man can also be ruled out as an important factor influencing the population dynamics since BCI has been left relatively undisturbed as a nature reserve since 1923. The island's flora and fauna have been studied intensively for many years (see, for example, Leigh *et al.*, 1982). The ecological setting in which these army ants exist, therefore, is well-known compared to similar tropical locations.

Of the 13 species of army ants known to inhabit BCI, *Eciton hamatum* and *E. burchelli* have been studied the most (Rettenmeyer, 1963a; Schneirla, 1971; Franks, 1982a). Considerable quantitative data on the activity cycle and raiding characteristics of *E. burchelli* on BCI have been accumulated (Willis, 1967; Franks, 1982a; Franks and Fletcher, 1983). The simpler raiding patterns of *E. burchelli* colonies compared to those of *E. hamatum* colonies (Schneirla, 1971:77-84) facilitate modelling of the former species; and the number of *E. burchelli* colonies on BCI has been estimated at least four times over three decades (Franks, 1982b). The composition of *E. burchelli's* diet and the rates of recovery of its various prey following a raid have also been measured on BCI (Franks, 1982a). Finally, the ecology of *E. burchelli* has been modelled before now (see section 3.1.4).

### 3.1.2 Relevant background information on *Eciton burchelli*

*E. burchelli foreli* Mayr (subfamily Ecitoninae) is a neotropical army ant ranging from Ecuador in the south to Honduras in the north (Watkins, 1976). Colonies have a single queen and from about 150,000 to 700,000 workers (Rettenmeyer, 1963a:369-370). Unlike many other species of army ants, *E. burchelli* is entirely epigaeic, (ie., restricted to above ground activity; Gotwald, 1982). Although colonies occasionally raid up into the trees (Rettenmeyer, 1963a:358, 361; Willis, 1967), they spend most of their time raiding and nesting at or near ground level.

#### a. Diet

*E. burchelli* appears to be entirely carnivorous, its diet on BCI consisting of about 50% social insects (mainly ant and wasp brood) and 50% other arthropods such as crickets, cockroaches and spiders (Franks, 1982a). Raiding *E. burchelli* colonies are also often accompanied by a host of other animals, notably antbirds (Willis, 1967) and parasitic flies (Rettenmeyer, 1961), which may attack a greater biomass of arthropods (other then social insects) than the army ants themselves (Franks, 1982a). Nevertheless, these arthropods are able to return to their former levels within a week (Franks, 1982a). This suggests that, except perhaps at exceptionally high densities of army ant colonies, the abundance of arthropods is unlikely to be limiting the army ants. The social insect prey on the other hand take almost 200 days to recover to their original levels and could

therefore be an important regulatory influence on *E. burchelli* (Franks, 1982a).

**b. Activity cycle**

*E. burchelli* colonies follow a 35 day activity cycle composed of a nomadic phase (NP) and a statary phase (SP). Each of these phases is characterised by a certain pattern of daily movement of the colony and by the stage of development of the current batch of brood within the colony. The following data are principally from Willis (1967).

During the statary phase, which lasts an average of 21 days, the queen lays in the region of 55,000 to 66,000 eggs (Hagan, 1954; cited in Rettenmeyer, 1963a:340,370), whilst the larvae that hatched at the end of the previous statary phase undergo pupal development. The simultaneous hatching of the eggs into larvae and the eclosion of the pupae into new adult workers coincides with (and probably triggers, according to Schneirla (1971:157); but see also Topoff *et al.*, 1980) the beginning of the 14 day nomadic phase. The new adult workers are called 'callows' because of their light pigmentation and soft exoskeleton. During the nomadic phase the larvae feed and grow until they begin to pupate, whereupon the next statary phase begins. Diurnal raids occur on only 13 days of the statary phase on average, and each raiding party retreats to the statary phase bivouac at dusk. During the nomadic phase, however, there are numerous larvae to feed, and raiding occurs on all 14 days. 86% of the nomadic phase days then terminate with an evening emigration

of the entire colony to a new bivouac site somewhere towards the end of that day's raiding trail. For the remaining 14% of nomadic phase days the raiding ants do not emigrate. Instead, they simply return to their current bivouac site and raid out in a new direction the next day.

**c. Swarm raids**

Schneirla (1940) and Willis (1967) described the spectacular swarm raids formed by *E. burchelli*. A well-developed swarm raid consists of up to 200,000 ants, most of which search through the leaf-litter in the composite form of a crescent shaped front up to 15m across (6m on average; Willis, 1967). Behind the front, the swarm tapers to form a single column of ants which trails back to the bivouac comprising the remaining two thirds of the colony. Although the raid-front occasionally turns to one side and then the other as it advances, the successive turns tend to compensate for one another in such a way that the original direction of progress is generally maintained throughout the raid (Rettenmeyer, 1963a:361; Schneirla, 1971:84; Franks and Fletcher, 1983).

Raid distances and angles are shown in Table 3.1. The large angles between successive raids in the statary phase result in a spoke-like arrangement of former raid trails centred on the bivouac. The raid trails of successive statary phases rarely overlap, however, because successive nomadic raids and emigrations tend to follow the same compass bearing (Franks and Fletcher, 1983). There is

probably no correlation between the overall direction of one nomadic phase and that of the next (N.R. Franks, pers. comm.).

**Table 3.1 Data on raid characteristics gathered for *Eciton burchelli* on Barro Colorado Island, Panama. (Positive and negative angles refer to clockwise and anti-clockwise deviations respectively.)**

| Model parameter | mean | standard deviation | sample size | reference |
|---|---|---|---|---|
| **Nomadic Phase** | | | | |
| raid distance | 116m | 48m | 38 | Franks (1982a) |
| emigration angle 1 | +8° | 52° | 56 | Franks and Fletcher (1983) |
| emigration angle 2 | +33° | 99° | 9 | Franks and Fletcher (1983) |
| emigration distance | 81m | 43m | 395 | Franks (1982a) |
| **Statary Phase** | | | | |
| raid distance | 89m | 41m | 25 | Franks (1982a) |
| raid angle | -123° | 40° | 41 | Franks and Fletcher (1983) |

**Note:** In the nomadic phase, emigration angle 1 refers to the angle between immediately successive emigrations; and emigration angle 2 refers to the angle between delayed emigrations.

### 3.1.3 The population dynamics of *Eciton burchelli* on BCI

The results of four different attempts to census the number of colonies on BCI are shown in Table 3.2.

**Table 3.2 Estimated number of *Eciton burchelli* colonies on BCI over 30 years. (The estimate by Franks (1982b) represents a mean with a standard error.)**

| Census Year(s) | Estimated Number of Colonies | Census Technique | Reference |
|---|---|---|---|
| 1949 | 45 | Queen marking. | Schneirla (1949) |
| 1955 | 50 | Queen marking. | Schneirla (1956a) |
| 1961-2 | 50 | Counted the number of statary phase bivouacs within a study area. | Willis (1967) |
| 1978-9 | 55 ± 5.2 | Based on that of Newman (1966) for estimating the length of plant root systems. | Franks (1982b) |

Two problems must be addressed. First, the accuracy of the census techniques mentioned in Table 3.2 should, where possible, be estimated. Second, on the assumption that the censuses were, in fact, accurate, an explanation must be sought for the apparent stability of the population of *Eciton burchelli* at about 50 colonies for some 30 years. BCI has an area of 15.6km², giving an average density of 3.2 colonies per square kilometre.

Such apparent constancy of the total population size stands out against the seasonal and annual fluctuations exhibited by many other arthropods on BCI (Willis, 1976; Wolda, 1978a,b; Levings and Windsor, 1982), and in the tropics and temperate zones in general (eg., Janzen and Schoener, 1968). It is difficult to compare this constancy with other social insects, however, because of the enormous

gap in our knowledge of social insect population dynamics. Nevertheless, one would expect most adverse affects to be initially buffered by reductions in colony sizes rather than colony number.

**a. Reproductive capacity**

Reproduction in *E. burchelli* is almost totally confined to the dry season (Schneirla, 1948; 1971:199-201). In the dry season of 1946 sexual broods were found in six out of 18 (33%) *E. burchelli* colonies on BCI; and in the dry season of 1948 sexual broods were found in four out of 18 (22%) colonies in Panama (mainly BCI) (Schneirla and Brown, 1952). These data for the two years are not significantly different (chi-squared = 0.55 on 1 df; $0.5 > P > 0.1$); and pooling them results in 10 out of 36 colonies (28%) with sexual broods. It appears, first, that only the largest colonies produce sexual broods (Franks, 1982a, 1985), and second, that colonies will always divide if they have sexual brood. Colonies certainly always seem to produce females in addition to male sexuals (Schneirla, 1971:204), and at least one new female is required if one of the daughter colonies is to have a queen. Thus probably around 20 to 30% of the colonies fission each year during the dry season on BCI (ie., 10 to 15 or so in a population of 50 colonies).

Colony fission never results in more than two daughter colonies (Schneirla, 1956b; Franks and Hölldobler, 1987). One of these daughter colonies is inherited by a new queen, and the other is either inherited by the old queen or by

another new queen if the old queen is rejected by the workers. Both the daughter colonies are approximately equal in size (Schneirla, 1956b; Franks, 1985).

Unchecked by deaths or fusions, one third of the colonies reproducing each year would result in an exponential population doubling time of merely 2.4 years (ie., $\log(2) / \log(1 + {}^{1}/_{3})$).

**b. <u>Predation, parasites and diseases</u>**

No specific parasites or diseases of *E. burchelli* are cited in the literature, although the brood are conceivably susceptible to attack by fungi, bacteria or nematodes (Bequaert, 1922a). Parasites have certainly been recorded in ants (reviewed in Hölldobler and Wilson, 1990:489-490, 554-555), but their potential for population regulation has not been investigated. The parasitic flies that hover over the swarm front of an *E. burchelli* raid apparently attack the large arthropod prey flushed out by the army ants rather than the ants themselves (Rettenmeyer, 1961).

No important predators of *E. burchelli* appear to exist on BCI, although both vertebrates and invertebrates are known to attack army ants (reviewed in Bequaert, 1922b, and Gotwald, 1982). Certain beetles prey on army ant brood (eg., Akre and Rettenmeyer, 1966; Akre, 1968; Plsek *et al.*, 1969; Topoff, 1969) and have been observed to stimulate cannibalism of the brood by the adult army ants themselves (Akre, 1968). Despite great variation among colonies (Rettenmeyer and Akre, 1968), the numbers of such predators

and scavengers associated with any one *E. burchelli* colony appear to be very low (eg., no more than one staphylinid beetle per 1000 ants; Akre and Rettenmeyer, 1966). It is unlikely, therefore, that they regulate the population dynamics of *E. burchelli* on BCI.

Other myrmecophiles associated with the army ant colonies (eg., mites, diplopods, collembolans, thysanurans, phorid flies and diapriid wasps; Rettenmeyer, 1962a,b, 1963b; Akre and Rettenmeyer, 1968) appear only to scavenge refuse deposits and booty of the army ants, and may even benefit the ants by keeping their bivouacs clean of fungi and organic debris (eg., Rettenmeyer, 1962b; Rettenmeyer and Akre, 1968). The antbirds that follow the colonies feed primarily on the arthropods flushed out by the ants rather than on the ants themselves (Rettenmeyer, 1963a:362).

**c. <u>Interspecific competition</u>**

It has already been mentioned in section 3.1.2a that although the various animals accompanying a swarm raid of *E. burchelli* consume a greater biomass of the prey flushed out by the army ants than the ants themselves, the arthropods are able to return to former levels within a week (Franks, 1982a). Further, the swarm attendants only appear to be taking the prey that would otherwise escape the army ants; Rettenmeyer (1963a:356) estimated that 30% to 50% of the arthropods flushed out by *E. burchelli* escaped the ants. Many of the swarm attendants would also be predicted not to compete severely with the army ants, simply because they

depend on the ants to flush out a high proportion of their prey (see Table 2 in Franks, 1982a).

The diets of other forest floor insectivores on BCI, such as the lizard *Anolis limifrons* and the coati *Nasua narica* (both of which are far more abundant per hectare than *E. burchelli*), appear to overlap little with that of *E. burchelli* (Franks, 1982a). This leaves other ants, particularly other army ants, as the prime contenders for interspecific competition with *E. burchelli*. Most of the remaining 12 species of army ant on BCI are far less conspicuous and well-known, restricting most of their activity to below the ground. Two notable exceptions are *Eciton hamatum* and *Labidus praedator*, both of which appear to be more common than *E. burchelli* on BCI (Willis, 1967; Schneirla and Brown, 1950). However, *E. hamatum* specialises more on social insect prey than other arthropods (Willis, 1967); and *L. praedator* appears to feed on arthropod prey smaller than the prey of *E. burchelli* (Rettenmeyer, 1963a:404; Willis, 1967) and spends more time raiding at night and underground (Rettenmeyer, 1963a:406,410; see also Schneirla, 1949, for a comparison of the diets and raiding activity of the three species).

**d. Deaths and fusions of *Eciton burchelli* colonies**

Queenright colonies of army ants will not tolerate each other. Although little fighting breaks out among their workers whenever two colonies meet, their workers do stand off from each other and their lines of traffic are re-routed

(Schneirla, 1940; Schneirla and Brown, 1950; Rettenmeyer, 1963a:323; Schneirla, 1971:79, 180). Colonies that have lost their queens (through senescence, accident or predation), however, can suffer one of three fates.

First, if the queenless colony encounters a queenright colony of the same species (or even another queenless one; Schneirla, 1949), the two colonies will actually fuse to form a single colony (Schneirla and Brown, 1950). The brood of the original queenless colony is then devoured (Schneirla and Brown, 1950; Rettenmeyer, 1963a:310; Schneirla, 1971:180). Very few natural colony fusions have been observed (Schneirla and Brown, 1950).

Second, if the colony was rearing a sexual brood in the dry season when its queen had died, then the colony could, in principle, simply adopt one of the new daughter queens to emerge from the brood once she has mated.

Third, however, if the worker brood have matured into adults before the queenless colony has fused with a queenright colony, then the organization of the colony seems to disintegrate and the colony apparently dies (Schneirla and Brown, 1950).

Presumably, colonies also die if they become too small to present an effective raiding force (see section 2.3.2 in chapter 2, and also Schneirla, 1949). Estimates of minimum colony size for *E. burchelli* vary considerably in the literature: from 40,000 (Schneirla, 1949) through 150,000 (Rettenmeyer, 1963a:369) to 280,000 workers (Franks, 1980:57). Rettenmeyer (1963a:305) admitted his methods of

estimation were 'subject to considerable error', and Schneirla's techniques were probably similar. Therefore I shall assume Franks's (1980) estimate to be the most reliable but still allow for considerable flexibility. Although natural colony deaths are very rarely observed (eg., see Schneirla and Brown, 1950), they would probably go unnoticed if they occurred rapidly or were restricted to small, relatively inconspicuous colonies.

**e. Population dynamics: summary**

In brief, the population of *E. burchelli* colonies on BCI appears to have remained constant over many years despite a massive reproductive potential and the apparent absence of any observed natural colony deaths or fusions. In this case, predation, parasitism, diseases and interspecific competition are unlikely to be significant regulatory factors. One major alternative remains: intraspecific competition. The importance of this was initially explored by means of a sophisticated simulation model which will be described after previous modelling attempts have been reviewed.

### 3.1.4 Previous models

The complex model described in this chapter is partially based upon the only other model that has been designed to investigate the ecology of *E. burchelli*, namely the model developed by Franks and Bossert (1983). In the latter model, the army ant colonies were treated simply as mobile

entities, incapable of growth, death or reproduction; the main purpose of the model being to estimate the impact of the army ants on the forest floor. Franks and Bossert modelled the movement of the colonies over a range of colony densities within a simulated area of 1 $km^2$ which was divided up into 10,000 square patches 10m on a side. The foraging area was effectively without edges (colonies that went off one edge reappeared on the opposite edge); and the colonies were programmed to stop raiding upon encountering patches raided by other colonies within the last 20 days. If the colonies did not do this then they were found to collide at a much higher frequency than observed (see section 3.2.1 below also). One of the major findings of the model was that, at a simulated density of colonies comparable to that found on BCI, approximately half of the patches had been raided in the last 240 days. This discovery will be considered again in the next chapter (section 4.3.2).

## 3.2 Methods: description of the model

The models in this and the next chapter were written in the programming language Turbo C (Borland, USA) on an Opus 386SX personal computer with an 80387 maths coprocessor and 1Mb of RAM.

### 3.2.1 Activity and movement patterns

Unlike the Franks and Bossert (1983) model, the entire surface of BCI was modelled explicitly; henceforth, therefore, this model will be referred to as the 'BCI

model'. The surface was sub-divided into square patches 12m on a side. Such dimensions were both biologically reasonable and also allowed the whole of BCI to fit onto a monitor screen of resolution 640 x 480 pixels, with one pixel for each patch. An area of 144m² was therefore the minimum unit of occupancy for a model colony of *E. burchelli*.

Although the lengths of the statary and nomadic phases were fixed at 21 and 14 days respectively, the movement angles followed normal distributions with the same means and standard deviations as the empirical data in Table 3.1. The maximum raid distances for the statary and nomadic phases, and the emigration distance in the nomadic phase, were given the observed mean values of 89m, 116m and 81m respectively (Franks, 1982a).

Colonies laid chemical pheromone trails which were programmed to decay as they did in nature (Schneirla, 1940; Topoff *et al.*, 1972, 1973; Torgerson and Akre, 1970a,b). Some evidence suggests that *E. burchelli* colonies avoid one another's pheromone trails (Willis, 1967; Franks, 1982c; Franks and Bossert, 1983; Franks and Fletcher, 1983). Despite several anecdotal records of colonies of other species of army ants interpreted as *following* the trails of other colonies (Schneirla and Brown, 1950; Schneirla, 1971:77), conspecific trail following has not been reported in *E. burchelli* (Franks and Fletcher, 1983). Furthermore, no direct collisions between *E. burchelli* colonies have ever been observed in more than a 1000 nomadic raids (Franks and

Bossert, 1983), even though collisions between *E. burchelli* and the more common *E. hamatum* colonies have frequently been observed on BCI (Franks and Fletcher, 1983).

As in Franks and Bossert (1983), therefore, colonies that encountered another colony or its trail pheromone were programmed to abort their raiding, retreat to their bivouac, and raid out in a new direction the next day (mean = +33°; s.d. = 99°; n = 9; Franks and Fletcher, 1983). Unfortunately, the time it takes for the pheromone trail to decay is not known precisely or is highly variable; estimates range from two days (Torgerson and Akre, 1970a) to 39 days (Rettenmeyer, 1963a:333).

Colonies were programmed not to raid on certain days of the statary phase based on data reported by Willis (1967). Model colonies that hit the coastline merely continued their raids along the edge of the island.

### 3.2.2 Growth, reproduction and death of the colonies

At the end of every statary phase, each colony received a fixed number of new recruits representing the newly emerged callow workers. During the fixed 130 days of the model dry season any colonies that surpassed a certain threshold size divided into two independent daughter colonies equal in size. Queens died once they outlived a certain, fixed age and their colonies then died if, by the time all their brood had matured, they had still not encountered and fused with another colony. Colonies that fell below a threshold size also died.

### 3.2.3 Patches: their impact on the colonies and the rate at which they recovered following a raid

Model army ant colonies suffered pre-defined levels of worker mortality (due to starvation or combat with the defending prey) when they raided across patches of forest floor. The age of every 144m² patch on the island was incremented by one day at the end of every day but the age of a patch was reset to zero following a raid. Patches in which the large arthropod prey had not yet recovered were assigned a certain colour and after a predetermined number of raid-free days these patches changed colour to represent patches in which the large arthropod prey (but still not the social insect prey) had now recovered. If yet more time passed without the patches being re-raided, then they changed colour again when the social insect prey had recovered. The colonies were programmed neither to avoid nor seek out patches of certain types, in common with findings for real army ants (see Mirenda *et al.*, 1982).

### 3.2.4 Initialisation of a simulation

The user defined the initial sizes of the colonies (which were all identical), the number and location of the colonies on BCI, the rate at which their trail pheromones decayed to undetectability, and the size thresholds that determined when a colony would die or reproduce. All the patches on BCI were initially set to the fully recovered state. To create a more realistic patch set-up, therefore, all the colonies were allowed to raid over the island for a

predetermined period. Thereafter the simulation proper began, with colonies only then being allowed to age, grow, reproduce and die.

## 3.3 Results

### 3.3.1 Evaluation of the census techniques

1) Schneirla (1949, 1956a) simply distinguished the queens he caught with different marks and made rough estimates of population size. His census technique was therefore not modelled.

2) Willis (1967) counted 12 statary bivouacs over 11 months of search within a 0.4km² rectangular study area (see Fig. 3.2), indicating a population of about 50 colonies on BCI in 1961-1962. (11 months, or about 330 days, is roughly equivalent to 330/35 = 9.43 activity cycles. Thus if the density was one colony per 0.4 $km^2$, Willis would have seen 9.43 statary phase bivouacs. But he saw 12, indicating a density of (12/9.43)/0.4 = 3.18 colonies per $km^2$, or 3.18 x 15.6 = 49.6 colonies on BCI as a whole.)

Table 3.3 shows the model's census results obtained using Willis's technique for different pheromone trail decay times after 50 randomly placed colonies were allowed to move over the surface of BCI, with no growth, death or reproduction.

3) Franks (1982b) based his census technique on a formula invented by Newman (1966) for estimating the total length of plant roots in a sample:

$$S = \pi.N.A \;/\; (2L)$$

**Table 3.3 Number of colonies on BCI as estimated by simulations of Willis's (1967) census technique.**

| Pheromone trail decay time / days | Census estimate Mean | s.d. | n | range | Result of t-test |
|---|---|---|---|---|---|
| 1 | 45.8 | 13.5 | 17 | 21-66 | NS(P > 0.10) |
| 6 | 45.3 | 14.8 | 12 | 12-66 | NS(P > 0.10) |
| 35 | 39.6 | 12.1 | 12 | 17-62 | 0.02>P>0.01 |

**Note:** The t-tests test for a significant difference between the mean estimated number of colonies on BCI and the real number, fifty (Bailey, 1981).

*N* is the number of intersections a line of length *L* will make, whatever its shape, with randomly scattered lines of total length *S* within an area *A*. Franks used the number of intersections, *N*, that the *E. burchelli* raids of unknown total length *S* made with a known length of footpaths, *L*, on BCI of area *A* (see Fig. 3.2). The number of colonies raiding on a given census day was estimated by dividing *S* by the average length of raids expected for the time of day at which the census was half completed. The result was then divided by the average proportion of colonies that raid on any single day to arrive at the final estimates of total population size. Over 1978-1979 he obtained an average census result of 55.0 colonies on BCI (sd = 11.56; n = 5). Table 3.4 shows the results obtained with the model for 50 colonies and different pheromone trail decay times:

**Table 3.4 Number of colonies on BCI as estimated by simulations of Franks's (1982b) census technique.**

| Pheromone trail decay time time / days | Running average of daily census estimate after 10,000 days |
|---|---|
| 1 | 45 |
| 6 | 47 |
| 35 | 47 |

Assuming the model closely replicated the movement patterns of real *E. burchelli* colonies on BCI then both Willis's (1967) and Franks's (1982b) census techniques appear to be quite accurate (although they slightly underestimated the true number of colonies), even allowing for great uncertainties in the trail pheromone decay time. Nevertheless, both Franks and Willis took relatively small samples (of five and one respectively) and the model clearly demonstrated the large variance in the results and the lack of confidence that should therefore be attached to any one census result.

Apart from emphasising the need for further censuses on BCI, however, I shall assume henceforth that the number of colonies of *E. burchelli* on BCI has been approximately constant at around 50 (in accordance with Schneirla's (1949, 1956a) intuition).

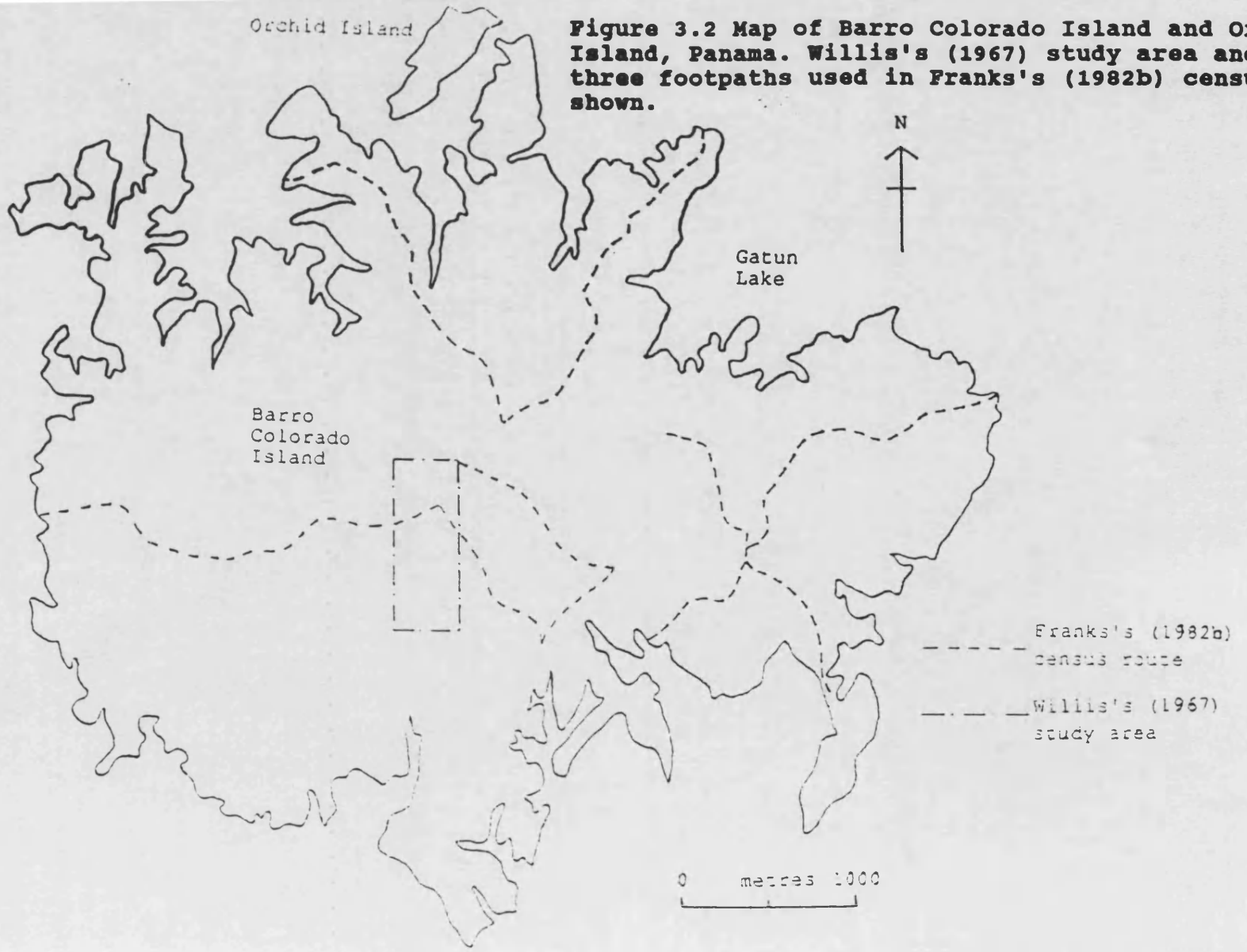



**Figure 3.2 Map of Barro Colorado Island and Orchid Island, Panama. Willis's (1967) study area and the three footpaths used in Franks's (1982b) census are shown.**

### 3.3.2 Achieving a stable model population

Originally, it was hypothesized that colonies would starve if they raided patches less than a week old (ie., patches in which the large arthropod prey had not yet recovered from a previous raid). It was also thought that colonies would sustain heavy losses due to combat with well defended nests of social insect prey in patches over 200 days old. For example, heavy combat casualties were observed in a colony of *E. burchelli* transferred to the previously virgin Orchid Island north of BCI (Franks, 1982a; see Fig. 3.2 also). Further, Droual (1983), LaMon and Topoff (1981), and McDonald and Topoff (1986) documented defensive behaviour in the ant prey of the north American army ant *Neivamyrmex nigrescens*; and Schneirla (1971:100) described the formidable resistance put up by many of the species of social insects preyed upon by army ants.

Thus it was assumed that patches of intermediate age were the most profitable (caused least mortality) because they provided sufficient food in the form of large arthropods and social insects to sustain colony growth, but did not support social insect colonies dense enough or large enough to inflict heavy casualties on the army ants.

However, such a model was not stable. Because the young patches only lasted a week, any mortality inflicted by them only became appreciable at very high densities (over 250 colonies on BCI). In any case, since the pheromone trail was also programmed to last about a week, few colonies could even venture onto the young patches without aborting

their raid. Colonies confined to peninsulas created and then repeatedly raided over areas of the intermediate aged patches that were favourable to population growth. Population explosions would thus ignite on the peninsulas and then spill over onto the mainland of BCI.

Moreover, at high densities colonies traversed relatively few patches each day before encountering another colony or its trail and aborting its raid. Thus they spent most of their time not raiding rather than suffering mortality in the young patches.

At the other extreme, once a population decline had started, extinction became virtually inevitable because of the growing proportion of fully recovered patches that inflicted very high mortality.

Overall, then, the model was very sensitive to the initial distribution of colonies and patches, and population change was inversely density dependent (small populations got smaller, big ones bigger).

Two main changes were therefore made to the model. First, the effects of the large arthropods on *E. burchelli* were ignored. Since they recovered so quickly they were unlikely to be regulating *E. burchelli* population size, in agreement with Franks (1980:84, 1982a). This effectively left two patch types in the model: ones in which the social insect prey had not recovered, and ones in which they had.

Second, to achieve density dependent population regulation, adverse effects have to, by definition, become proportionately more important as population size increases

(and vice versa). The level of army ant mortality associated with the patches up to 200 days old was therefore made to be greater, rather than smaller, than that associated with the older, fully recovered patches. This can be interpreted in biological terms by assuming that the high mortality due to combat with the defending social insect prey in fully recovered patches is more than offset by the relative abundance of food, particularly in the form of ant and wasp brood. By contrast, in patches where the social insects have not yet fully recovered, starvation of the army ants is severe even though there are few combat casualties.

However, if the population managed to reach locally high densities, population explosions could still not be prevented unless the colonies were also programmed to suffer mortality per unit time lost foraging. The biological justification for this was simply mortality due to starvation (see also Topoff and Mirenda, 1980a,b; and Mirenda *et al.*, 1982).

Incorporation of all these changes into the model finally resulted in density dependent regulation. Using the parameter values shown in Table 3.5 the population could be made to stabilise at around 50 colonies whether the initial number was 1, 50 or 100.

Interestingly, these results were hardly affected by variations, albeit minor, in the pheromone trail decay time, ranging between 1 to 6 days.

**Table 3.5 Typical parameter values that will achieve a stable population size of about 50 colonies in the BCI model.**

| | |
|---|---|
| Initial number of colonies: | 1, 50 or 100 |
| Initial siting of colonies on BCI: | random |
| Day on which colony growth, mortality, and reproduction can start: | 200 |
| Initial size of all the colonies (number of adult workers): | 350,000 |
| Net number of new adults produced at the end of every 35 days: | 60,000 |
| Queen lifespan (years): | 6 |
| Critical size of the colony at which fission will occur: | 500,000 |
| Threshold colony size at or below which a colony will die: | 200,000 |
| Adult worker mortality rate (as a fraction of total colony size) for a whole day spent not raiding: | 0.002 |
| Worker mortality due to collision with another colony: | 0 |
| Worker mortality due to the crossing of a patch in which neither the large arthropod nor the social insect prey have yet recovered: | 0 |
| Worker mortality in patches in which only the social insect prey have yet to recover: | 0.0006 |
| Worker mortality in fully recovered patches: | 0.0002 |
| Trail pheromone decay time (days): | 6 |
| Recovery time for the large arthropod prey (days): | 1 |
| Recovery time for the social insect prey (days): | 200 |

### 3.3.3 Colony movements and collisions

When the colonies were programmed to avoid only the trails of other colonies (and not their own trails as well) then no portion of the island was inaccessible to them in the long term, although colonies did occasionally become trapped on one of the peninsulas with narrow connections to the mainland. This finding corroborates Schneirla's (1971:76) observations that individual colonies were able to move over large areas of BCI.

Table 3.6 shows the effects of different trail pheromone decay times on the frequency of encounters between colonies in the nomadic phase and either other colonies, or the pheromone trails of other colonies. These results were derived from single simulations only, but they differed little from the results of repeated simulations in which the only differences were the runs of pseudorandom numbers used. In each case, 50 colonies were allowed to move over the island without growing, reproducing or dying.

The table shows that, as the pheromone trail decay time increased, the frequency of encounters of colonies in the nomadic phase with other colonies decreased, whilst the frequency of encounters with the trails of other colonies increased. Because the latter type of encounter increased faster than the former decreased, the net effect was an increased frequency of abortion of nomadic phase raids. Only when the pheromone trails took 20 days to decay did the percentage of NP raids that were aborted not differ significantly from Willis's (1967) results. Encouragingly,

**Table 3.6 The effects of pheromone trail decay time on collision rates. Collisions were recorded as encounters between colonies in the nomadic phase and either other colonies or the pheromone trails of other colonies. Willis (1967) observed 121, or 14.1%, of 860 NP raids to be aborted. The results of the three simulations are compared with Willis's (1967) result by means of the chi-squared test. The numbers of collisions are also expressed, in parentheses, as percentages of the total number of NP days simulated.**

| Pheromone trail decay time / days | Total number of NP days | Total number of collisions between colonies in the NP and: ...other colonies | ...the trails of other colonies | % of NP raids that are aborted: D = 100x (B+C)/A | Results of chi-squared test for difference of D from Willis's result |
|---|---|---|---|---|---|
| | A | B | C | D | |
| 1 | 296022 | 3461 (1.2) | 4718 (1.6) | 2.8% | P<<0.001 |
| 20 | 249636 | 1298 (0.5) | 30161 (12.1) | 12.6% | NS(P>0.5) |
| 40 | 345022 | 1390 (0.4) | 56915 (16.5) | 16.9% | P < 0.05 |

Franks and Bossert (1983) obtained the same result (see section 3.1.4). Further, for the 20 day decay time, the number of direct collisions between colonies in 1000 nomadic phase raids was only (1298/249636) x 1000 = 5.2, a figure not very different from the zero collisions for the more than 1000 nomadic raids that have been observed on BCI (Franks and Bossert, 1983).

These results can be contrasted with those of an otherwise identical simulation (ie., 20 day decay time) in which the colonies were programmed *not* to abort their raids upon encountering other colonies or the pheromone trails of other colonies. In this case, over half (54.4%) of the

total 362,203 nomadic raids encountered other colonies or their trails, and 17.2 collisions occurred between colonies out of 1000 nomadic raids.

Taken together, these findings are strongly consistent with the hypothesis that the 14.1% of nomadic raids observed to be aborted by Willis (1967) were aborted, (a), as a result of encounters with other colonies or their pheromone trails, and (b), that the pheromone trails are detectable by *E. burchelli* for approximately 20 days.

### 3.3.4 Colony fissions

Section 3.1.3a revealed that about one third of the colonies on BCI reproduced by fission each year. However, the frequency of fissions in the model was consistently lower than that observed when the empirical figures of 55,000 new callows eclosing every 35 days (Franks, 1982a), and a colony size threshold for fission of about 600,000 workers (Franks, 1980:57, 1985) were used. The observed fission frequency was achieved by changing two parameters. First, the size-dependent fission threshold was reduced to 500,000 workers. This also had the desired effect of causing at least some colonies to die of small size, whereas none had done so before. Second, the colony growth rate was increased to 60,000 new callows being produced every 35 days. Both of these adjustments were feasible in view of the high variance and uncertainty attached to the corresponding field measurements.

### 3.3.5 Colony deaths, dissolutions and fusions

When there were approximately 50 colonies on the model island, only about nine died per year due to falling below the threshold size. This accorded with the very few colony deaths that have been observed (see section 3.1.3d). Most of these deaths probably befell the relatively small daughter colonies produced by fission in the dry season (although some colonies may have died by becoming trapped on a peninsula and then repeatedly re-raiding patches in which the social insect prey had not yet recovered). Schneirla (1949) certainly believed that most colony deaths occurred during the dry season.

The frequency of colony dissolutions following queen death and a failure to locate and fuse with another, queenright, colony was even smaller, only about two deaths per year. Dissolutions are probably also inconspicuous, with the colony members presumably dispersed over a relatively large area and dissolution setting in rapidly once all the brood have matured.

Fusions occurred only slightly more frequently (between 3 and 4 per year) in the model than deaths by dissolution. This also corresponds with the very few fusions observed (see section 3.1.3d).

Note that 9 deaths, 2 dissolutions and 4 fusions sum to the loss of 15 colonies per year; ie., approximately one third of 50 colonies. Thus losses balanced gains on average and the model population was at equilibrium.

A comparison of the number of queens that died with the number of fusions, dissolutions and fissions revealed that, for example, over half of the colonies which lost their queens (mean = 58%; sd = 12%; n = 13) were saved from dissolution by fusion with other colonies, an event that became increasingly rare as population density fell. About 14% of the colonies (sd = 7%; n = 13) were saved by the adoption of a daughter queen reared from sexual brood produced before their former queen died; and the remaining 28% of the colonies that lost their queens (sd = 11%; n = 13) underwent dissolution. All of these predictions could be compared with empirical data gathered in the future.

### 3.3.6 Distances between successive statary phase bivouacs

The model could be tested by comparing its predictions with data not explicitly programmed into the model. For instance, in section 3.3.3, the frequency of collisions between colonies observed in the model was compared with data from the field. Another piece of information not programmed into the model, but for which field data exist, is the direct distance between successive statary phase bivouacs. E.O. Willis's raw data yield a mean for this distance of 530m (sd = 267m; n = 38). It was found that, by reducing the trail pheromone decay time in the model, the distance between successive statary phase bivouacs could be raised. However, the effect of this was small: even if the trail pheromone decayed in a little as one day, the distance was only 416m in the model (sd = 217m; n = 20,922),

significantly less than that observed by Willis (approximate t-test: $t' = 2.627$; $P < 0.01$; Sokal and Rohlf, 1981:411). Moreover, section 3.3.3 showed that reducing the pheromone trail decay time also raised the frequency of collisions between colonies and reduced the proportion of nomadic raids that were aborted. So, if manipulations of the pheromone trail decay time cannot account for the discrepancy, then what can?

It seems likely that the discrepancy is due in part to biased sampling: Willis appears to have conducted most of his studies in the central region of BCI (eg., see Fig. 3.2), whereas the model also recorded data for colonies confined to the peninsulas where successive statary phase bivouacs were more likely to be closer together. Another contribution to the discrepancy is the fact that the maximum nomadic raid distance of 116m fed into the model (see Table 3.1) was only the *average* of the distances measured in the field, and Willis (1967), for instance, measured one nomadic raid 260m in length. Thus the average length of nomadic raids, due to abortion of a proportion of them before they reached 116m in length, was almost certainly less than 116m in the model. The discrepancy between Willis's and the model's results with respect to the distance between successive statary phase bivouacs could therefore be reduced somewhat by incorporating variation into the maximum permissible nomadic raid length in the model.

### 3.3.7 Interesting results from the model

1) Even when there were 50 colonies on the model island there were usually one or more 'lacunae' or 'super-patches' - large areas of the island representing patches in the same state of recovery (eg. patches in which the social insect prey had not yet recovered). Lacunae occasionally had no colonies within them and, over time, they tended to move, merge, split and change in size and shape according to the movements of the colonies and the state of recovery of the patches within them.

The presence of lacunae in the model raises the interesting possibility that there may be areas of uniformity in the state of the litter floor fauna on BCI that extend beyond the immediate size of the 144m² patch defined in the model. Study of any real lacunae that exist and their macroscopic dynamics may therefore cast some light on the diversity and dynamics of litter floor communities.

Large lacunae may represent areas of significant colony growth or mortality, depending on the mortality values of the patches comprising them, and can therefore influence their own lifetime through their affects on local colony density. It must be remembered, however, that there are 12 other species of army ant on BCI and the combined movement and activity of these could potentially remove any large-scale community patterns in the forest floor.

2) The model was quite sensitive to changes in the value of the queen lifespan parameter. A greater value resulted in a

longer colony survival time and a greater average colony density. The greatest recorded age for an *E. burchelli* queen is 4 years 2 months (Rettenmeyer, 1963a:371), and Schneirla (1971:175) estimated that the average lifespan is at least 3 years. Unfortunately, little is known about the mean and variance in queen lifespan, despite its apparent significance for the population dynamics of *E. burchelli*. The fixed figure of 6 years shown in Table 3.5 was based on the two assumptions that each colony only reproduces once on average every 3 years and has just two opportunities to reproduce during its lifetime (Franks and Hölldobler, 1987). Queen lifespan is reconsidered in the next chapter too (section 4.3.5b).

3) If the different colonies were identified by unique colours on the screen and the products of a colony fission programmed to inherit the colour of their parent then, eventually, the population came to be dominated by just one or two colours. Early on in a simulation, when there was only one colony of each colour, the death of a colony meant the permanent loss of a colour. If a colony fissioned, however, there were now two colonies of that colour, thereby both reducing the chances of that colour being lost and also raising the likelihood of further colonies of that same colour being produced.

This implies that there would be a gradual loss of genetic diversity over time in the maternally inherited mitochondrial genome of the island population, assuming

there was some diversity in the original founding population. The significance for the genetic diversity of the nuclear genome in the population, however, would depend on the amount of genetic diversity in the males on the mainland surrounding BCI, and also on the extent to which they fertilise females on the island. If most of the males fertilising the females come from the island population itself, then inbreeding and loss of genetic diversity in the nuclear genome would result. That the population of *E. burchelli* on BCI could be reproductively isolated to some extent has important implications for its evolution and any attempts at conservation.

4) There seems to have been some evidence of population cycles. New colonies in the model were only produced in the dry season and early wet season, but losses of colonies due to small size, or dissolution or fusion following queen loss occurred throughout the year. As was mentioned previously (section 3.3.5), deaths due to small size would have been most expected to strike the small daughter colonies produced in the dry season, especially since the temporary increase in population size would have resulted in more patches in which the social insect prey had yet to recover. Dissolution, however, was probably most likely just before the onset of the dry season when colony numbers were lowest and hence when queenless colonies were least likely to encounter and fuse with queenright colonies. Because the computer took several seconds even to simulate a single day,

it took many hours to produce an appreciable amount of data worth analysing for population cycles. For this and other reasons (see section 3.4.3 below), the complex BCI model was put to one side in favour of simpler models that ran much faster on the computer.

## 3.4 General discussion

### 3.4.1 Value of the model

The exercise of creating the complex model and exploring its results has proved valuable in many respects. First, it has provided general validation for the various census techniques used, and hence supported the observation that the number of *E. burchelli* colonies on BCI has remained approximately constant at around fifty for some thirty years. This provided the necessary confidence for proceeding to the next step, namely, the explanation of that constancy. Second, it has been possible to achieve density dependent population regulation in the model with biologically reasonable values of the parameters, given the present uncertainty that exists about some of their values, such as the rate at which the trail pheromone decays. Third, the model has allowed inferences to be made about the values of at least one of these parameters, namely the trail pheromone decay time. Fourth, it appears that the large arthropod prey are relatively unimportant with regard to their affect on the population dynamics of *E. burchelli*. In contrast, the most important regulatory factor appears to be intraspecific competition among the army ant colonies for

the patches of habitat in which the social insect prey have fully recovered from previous raids by army ants. Fifth, the model has pointed to some interesting processes that may be occurring on the real BCI, such as 'super-patches', loss of genetic diversity, and population cycles. Sixth, the model has suggested which factors may be particularly important in affecting the population dynamics, such as queen lifespan, not to mention the mortality inflicted by particular patches.

In the future, the model could prove equally valuable in the development and refinement of specific hypotheses concerning the conservation of *E. burchelli* on BCI, or indeed, other islands (eg., nature reserves). The model could easily be altered to yield information about, for example, the distribution of colony sizes, something that could be measured on BCI.

### 3.4.2 Important assumptions

The model centres upon the assumption that density dependent population regulation is occurring. The density dependence was principally achieved by making patches that have been recently raided more harmful to the army ant colonies than older patches. The biological hypothesis erected to account for this was that the lower mortality incurred in younger patches by the army ants, due to combat with the defending social insect prey, was more than outweighed by the greater mortality through starvation. Conversely, older patches were presumed to be most beneficial to the army ants because

the food they acquired in these patches more than offset the greater combat mortality. This hypothesis needs to be tested.

Another important simplifying assumption made in the model was that the recovery of a patch neither affected, nor was affected by, the state of recovery of surrounding patches. If patch interactions were found to be important, then their effects on the army ant population dynamics could perhaps be investigated by developing cellular automata type models. Cellular automata consist of networks of interconnected units (such as patches), the future internal states of which are affected both by their own present states and also by the current states of the units to which they are connected.

### 3.4.3 Problems encountered

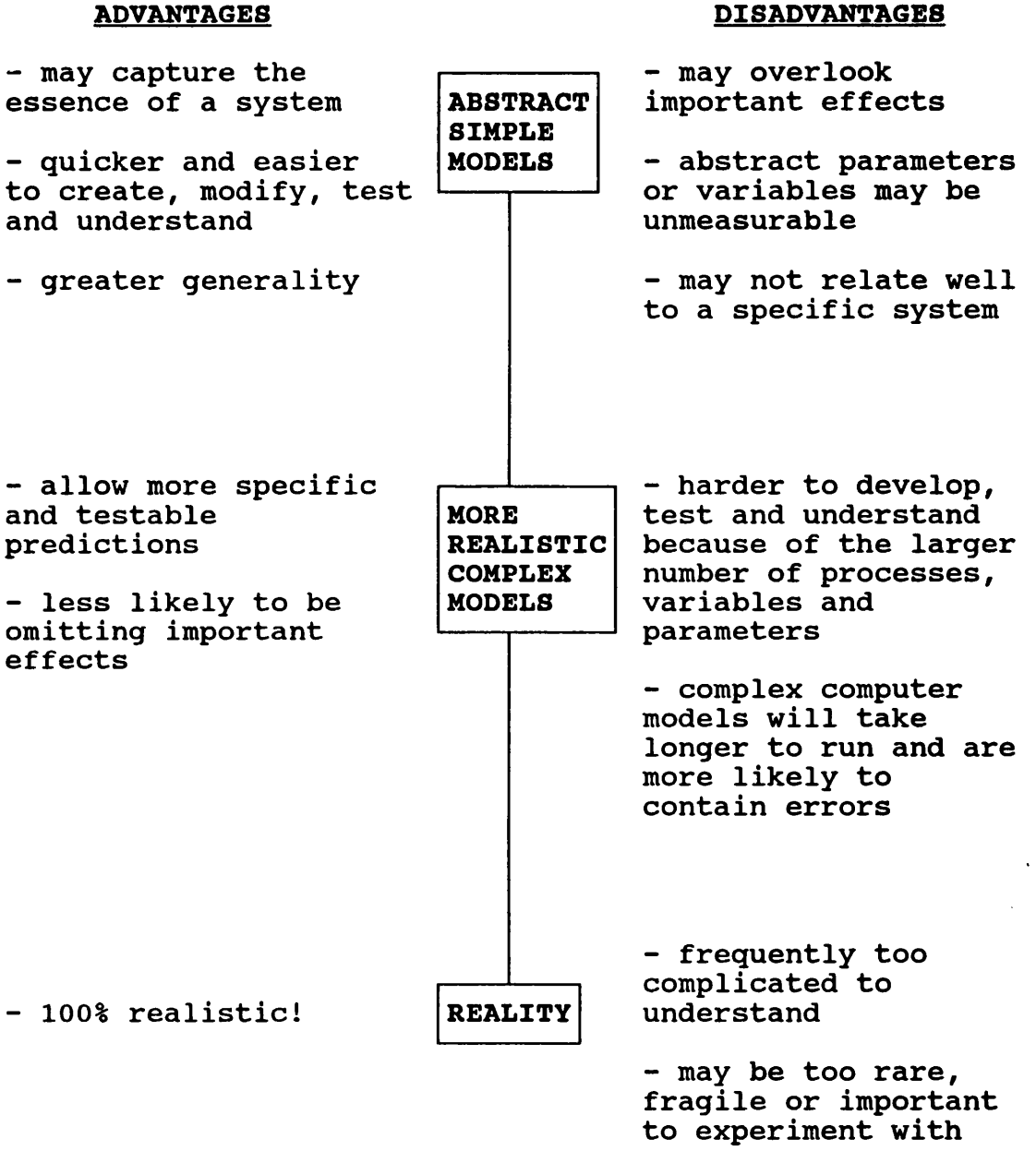
The advantages and disadvantages of complex and simple models are shown in Fig. 3.3. The two types of model should be regarded as complementary, as opposed to alternative, aids to the understanding of a system. A computer model is a tool that serves to help explore the ramifications of a hypothesis. Often, this hypothesis invokes one or more processes which are too complicated to describe or analyse on a mathematical basis, or which are difficult to interpret when expressed in mathematical terms. How complicated a model is made depends on what questions are intended to be answered; the object of a model is not to reproduce the complexities of reality, but to determine which components

of it can account for most of the phenomenon in question. Nevertheless, knowing what to include or omit from a model often leaves ample scope for individual judgement. Two further general problems were encountered during the development of the complex model.

First, programming errors were occasionally made. The worst type were those that produced an effect similar to the one expected of the correct program. Such errors are both more likely to occur and also to escape detection in long complicated programs.

Second, it was sometimes difficult to know which parts of the model should be allowed to vary whilst others were kept constant. For instance, the length of the activity cycle was fixed as a constant because it was believed that variation in it would hardly affect the general results of the model. However, the number of new callows produced every 35 days, the queen lifespan, and the size thresholds for death and reproduction were also represented as constants, and yet variation in these may have had important effects on the outcome of a given simulation. In principle, the model could be subjected to a sensitivity analysis - ie., an assessment of the sensitivity of its output to variation in the parameters and variables within it - but this obviously becomes very difficult and tedious for models with many parameters and variables. The next chapter describes the use of simpler, more abstract, models with far fewer parameters.

**Figure 3.3 Abstract, simple models versus more realistic, complex models; and their relation to reality.**



# Chapter 4

# The Population Dynamics of the Army Ant *Eciton burchelli*. II. Simple models and analytical equations

## 4.1 Introduction

The complex model of the previous chapter verified the census results and suggested how density dependent mortality might be acting upon the population. Yet the very complexity of the model made it difficult to analyse in detail. What was needed was a far simpler model of the army ant system. This chapter describes just such a model and also the results of an attempt to describe the simplified system by means of analytical equations. Rather than simply presenting the final model with no explanation of how it was derived, the structure of this chapter reflects the step-by-step way in which the model was developed.

## 4.2 The 'Grid' model

### 4.2.1 Assumptions and structure of the model

It was assumed first that some patches of the rainforest floor are 'good' in that they have net beneficial effects upon the army ant colonies raiding them, whereas all remaining patches have net harmful effects and are 'bad'. (Note the use of the term 'net'. Both types of patches may in fact cause an immediate reduction in the size of the army ant colony raiding them due to combat mortality or starvation. It is merely assumed that the food gathered from good patches results in the production of more than

enough workers to offset this loss at the end of the current 35 day activity cycle, whereas losses exceed production in the case of bad patches.) If the effect upon a colony of a good patch is also assumed to be equal and opposite to that of a bad patch then, at equilibrium, the probability of raiding a good patch must be equal to the probability of raiding a bad patch.

However, the difference in movement pattern between the nomadic and statary phases of the activity cycle strongly suggests that the patch-to-patch variation in the fortunes of a colony will be much higher in the nomadic phase than the statary. This is because the raids of the nomadic phase pass through large areas of rainforest and, therefore, at equilibrium, the army ants probably raid through just as many bad patches as they do good ones in a single nomadic phase. Thus the fortunes of a colony in different nomadic phases may be approximately constant and the nomadic phase cannot therefore be responsible for fluctuations in the population size.

In contrast, the rosette-like pattern of the statary phase raids are restricted to more or less the same area, and consequently there is a much greater chance that the whole statary phase is confined to an area consisting mostly or entirely of patches of one kind. In other words, the fates of individual colonies, and hence the fate of the entire population, depend upon their fortunes in the statary phase. These assumptions seem reasonable even if the good

and bad patches are not distributed entirely at random over the island's surface.

Based on these assumptions an abstract model called 'Grid' with the following features was constructed:

1) The island was represented by a square grid of patches wrapped into a seamless surface so that colonies disappearing off one 'edge' simply reappeared on the opposite 'edge' of the grid (just as in the Franks and Bossert (1983) model).

2) Each square patch represented the area encompassing an average rosette of 13 statary phase raids. Since an average statary phase raid is 89m long (see section 3.1.2b), the squares were 2 x 89m = 178m on a side (and therefore 31,684$m^2$ in area).

3) The basic time step was now 35 days, the average length of the activity cycle for *E. burchelli*. The model stepped from the end of one statary phase to the end of the next, 35 days later.

4) At every time step the model colonies took turns to 'jump' from one square patch to another, such that the distance jumped was approximately equivalent to the average observed distance between successive statary phase bivouacs, 530m (Willis, 1976; see section 3.3.6 also). Colonies therefore jumped from their current patch to another one 530m/178m = 2.98 or 3 patches away. Colonies moved independently of one another (apart from the order in which they moved) and more than one colony could occupy a patch. Colonies neither sought nor avoided patches of a particular

age. The direction a colony took was selected at random from 1 to 360$^{o}$ and although a whole square was always raided, the colony occupying it was not necessarily in its centre.

5) Colonies were only allowed to have discrete sizes in the range 0 to 10 size units. Any colonies that fell to zero units in size died, and any that reached size 10 divided into two daughter colonies of size 5 each.

6) At the end of every time step the ages of all unoccupied patches were incremented by one time step. As in the revised version of the BCI model (see section 3.3.2), the non-social arthropod prey were ignored, and it was assumed that the social insect prey took 6 time steps (6 x 35 = 210 days) to recover from a raid by army ants. Thus all patches 6 time steps or less since the last raid were called 'young' patches; the rest were 'old'. Density dependent population regulation was achieved in a slightly different way to the BCI model. In the BCI model, recruitment was constant and colonies always suffered mortality when raiding patches; they simply suffered less mortality in the old patches than in the young patches. In the Grid model, however, colonies lost one size unit if they raided young patches but gained one size unit if they raided old ones (the effects that a patch and a colony had upon each other were assumed to be independent of the size of the colony raiding the patch). Thus, if, for example, the population size increased for some reason, the number of

young patches would then increase and mortality would consequently rise, resulting in a fall in population size.

### 4.2.2 Preliminary results

Most simulations were begun with a single colony of size 5 units in the centre of a 20 x 20 grid of old patches. The colony grew and divided at first when virtually all the patches it raided were old. However, the rate of population growth decreased as the number of young patches increased with larger numbers of colonies, and the population size eventually began to fluctuate within relatively narrow bounds.

Reruns of simulations using the same parameter values and initial setup but with different seeds for the pseudo-random number generator produced very similar results. Judging from the means of various variables, the simulations generally stabilised by 500 time steps. Table 4.1 below shows the results of two such simulations.

The number of colonies and young patches, average patch age and average colony size all exhibited significant autocorrelations, although time series plots showed that the periodicity was not very regular. For an island of 20 x 20 = 400 patches in size, for example, the population size fluctuated between about 30 and 45 colonies and the number of young patches between about 150 and 210. All the cycle lengths were about 40 to 42 time steps. The cycles appeared to be stable limit cycles in that the system converged upon them from very different initial numbers of colonies.

**Table 4.1** Mean values of some variables from two different runs of the Grid model (time steps 501 to 4000; ie., n = 3500). (This is the 'J' type version of the model; see section 4.2.3 below for an explanation.)

| Variable | Mean Values | |
|---|---|---|
| | Run 1 | Run 2 |
| No. of colonies: | 37.2 | 37.5 |
| No. of young patches: | 185.3 | 186.7 |
| Colony size: | 5.0 | 5.0 |
| Patch age (time steps): | 10.9 | 10.8 |
| No. of births per time step: | 0.86 | 0.85 |
| No. of deaths per time step: | 0.86 | 0.85 |

Island size (whilst keeping the shape constant as a square) was varied between 100 and 400 patches. There were no significant changes in average patch age or average colony size, but there were positive linear relationships between island size (number of patches) and both the mean number of young patches and the mean number of colonies. Cycle lengths were hardly affected.

### 4.2.3 Altering the distance between successive statary phase bivouacs

To what extent were these findings influenced by the distance between successive statary phase bivouacs? One would predict that a small distance would increase the probability of a patch being re-raided by a colony before the patch has recovered from a previous raid by that same colony. This is because if a colony can only jump a short

fixed distance then it has fewer potential patches available for occupation on a given move than a colony that can jump a greater fixed distance.

To investigate the role of distances between successive statary phase bivouacs, the Grid model was modified so that colonies could only move one square at a time in any one direction. Thus a colony could now only enter one of the eight squares immediately adjacent to its current patch. The modified model was called the 'S' or 'Stepping' model to distinguish it from the 'J' or 'Jumping' Grid model considered earlier, in which the colonies could move or 'jump' into any one of the 24 squares a distance of three squares away. Although the S model was less realistic than the J model, the S model has provided some useful insights.

**Results**

Table 4.2 below shows the results of two simulation runs of the S model. The results can be compared directly with those of the J model in Table 4.1 because the initial setups and parameter values were identical. As before, the reruns were very similar and the mean values had virtually stabilised by 500 time steps into the simulation.

A comparison of Tables 4.1 and 4.2 shows that in passing from the J to the S model with an island of 20 x 20 patches, the following changes occurred (the statistics in parentheses refer to comparisons of the results of the first runs in Tables 4.1 and 4.2):

**Table 4.2** Mean values of some variables from two different runs of the 'S' version of the Grid model (n = 3500; time steps 501 to 4000).

| Variable | Mean Values | |
|---|---|---|
| | Run 1 | Run 2 |
| No. of colonies: | 27.2 | 27.0 |
| No. of young patches: | 134.0 | 133.4 |
| Colony size: | 5.1 | 5.1 |
| Patch age: | 19.1 | 19.0 |
| No. of births per time step: | 0.78 | 0.79 |
| No. of deaths per time step: | 0.78 | 0.79 |

1) The numbers of colonies and young patches fell by 27 to 28% (in both cases $P < 0.0001$ by the approximate t-test).

2) Average patch age rose by 76% ($P < 0.0001$ by the approximate t-test).

3) Birth and death rates fell, but only by about 8.5% (the respective P values from the Mann-Whitney test were 0.0014 and 0.0004).

4) Average colony size hardly changed (it rose by less than 1%; $P = 0.0003$ by the approximate t-test).

Variances in the number of young patches and average patch age also rose massively and any periodicity in the variables persisted only weakly or vanished altogether. Cyclicity in the original J model could also be diminished by making the model less discrete and more continuous in one or both of two ways. First, the colonies could be allowed to occupy a greater range of size classes (eg., 0 to 20 units), thus reducing the relative impact a single patch had

on a colony's size. Second, patch recovery could be made somewhat more continuous by introducing a third type of patch intermediate in age and impact on the colonies between the young and old patch types (age 3 to 6 time steps; impact = zero).

## 4.3 Analytical models

### 4.3.1 Introduction

To understand the results of the J and S versions of the Grid model and to further the understanding of the real army ant system, I enlisted the aid of Dr. Nick F. Britton, a biological mathematician at the University of Bath. Specifically, the aim of the collaboration was to develop analytical models of the army ant population dynamics that were both simple and mathematically tractable. The beauty of analytical equations lies in their explicitness, in their revelation of, first, what parameters are important (and just as importantly - what parameters are not important), and, second, the relationships between those parameters. This last point enables a researcher to make precise quantitative predictions and also suggests how sensitive those predictions will be to variations in the parameters.

For the purposes of this thesis it is not necessary to describe the detailed structure of the various models developed by Britton. The models centred upon two sets of equations: one set to describe the proportion of patches that were occupied at time step $t$ by colonies of size $i$ units; and another set to describe the proportion of patches

of age *j* at time *t*. All the equations were difference equations since they modelled the discrete passage of time from one step to the next (ie., from the end of one statary phase to the end of the next, just as in the Grid model). To simplify the analysis, all of Britton's models were deterministic.

### 4.3.2 A non-spatial model

The first model developed by Britton was a non-spatial analogue of the Grid model, in which the colonies could effectively jump to any patch on the island with equal probability, subject to the constraint that no more than a single colony could occupy a patch. The elimination of space from the system not only simplified the analysis but also isolated the temporal features of the system from the spatial features, thus allowing one to judge the relative importance of space and time in the population dynamics of army ants. The constraint was added because it was assumed that, since no collisions between *E. burchelli* colonies have ever been reported, colonies generally avoided each other and therefore would not establish statary phase bivouacs in the same patch (see also sections 3.2.1 and 3.3.3). Thus the probability of a colony raiding a patch of age *j* in Britton's non-spatial model was simply the proportion of the patches on the island that were of age *j* and unoccupied (and since this proportion at time *t* could only be one value, the model was still deterministic rather than stochastic). Apart from the ability of the colonies in Britton's non-

spatial model to jump to any unoccupied patch on the island, the only other difference between Britton's models and my Grid models was this constraint in Britton's models that patches could not be occupied by more than one colony. It will be seen later (section 4.3.6a) that this constraint makes little difference to the results. In all other respects his models were as similar to my Grid simulation models as possible.

Only 3 parameters were required in Britton's non-spatial model:

1) $K$, the number of patches on the island (and even this parameter can be omitted if the results are described in terms of proportions rather than numbers of patches).
2) $n$, which is a function of the rate at which the social insect prey recover from a raid by *E. burchelli*: young patches are of age $n$ (typically six) time steps or less, the rest are old.
3) $m$, the size of the daughter colonies produced by fission; a colony divides when it reaches a maximum size of $2m$ units.

Britton used these parameters and the two sets of equations mentioned in section 4.3.1 to arrive at a description of the system at equilibrium (see equations 4.1 to 4.7 below). Using matrix algebra he was then able to show that at equilibrium the system was on the borderline between stability and instability, but was unable to prove exactly which. Numerical attempts to find approximate solutions to the stability equations, however, suggested that the system exhibited damped oscillations to the steady

state over a long period of time. If $x^*$ is the proportion of patches on the island that are occupied by colonies at equilibrium, and $y^*$ the equilibrium proportion of patches that are young, then the following predictions were found to hold for equilibrium:

1) Number of colonies = $K.x^* = K.[1 - (1/2)^{1/(n+1)}]$ Eq.(4.1)

2) Number of young patches = $K.y^* = K/2$ Eq.(4.2)

3) Colony size: mean = $m$; Eq.(4.3)

variance = $(m^2-1)/6$ Eq.(4.4)

4) Patch age: mean = $(1 - x^*)/x^*$; Eq.(4.5)

variance = mean/$x^*$ = $(1 - x^*)/x^{*2}$ Eq.(4.6)

5) Number of births per time step = number of deaths per time step = (number of colonies)/$(2m^2)$ = $K.x^*/(2m^2)$ Eq.(4.7)

First, equation 4.1 demonstrates a simple linear relationship between island size and equilibrium population size; halving the number of patches, for example, will halve the number of colonies at equilibrium. Second, and in accordance with intuition, the equation shows that the equilibrium population size declines as patch recovery rates fall: poorer habitats support smaller populations. Because of the asymptotic shape of equation 4.1, however, a given change in $n$ has less proportionate affect on $x^*$ for large $n$ than small $n$. Thus, for $n > 4$, say, the equilibrium population size is relatively insensitive to variations in habitat quality. For example, if $n = 5$ (175 days) then $x^*$ is about 11%, but if the social insect prey take longer to recover and $n = 7$ (245 days), then $x^*$ only falls to about 8%

of the patches occupied. The corollary of this is that a rough estimate of population size can accommodate a wide range of possible patch recovery rates.

Equation 4.2 shows that the equilibrium number of young patches is constant and equal to half the patches on the island (in agreement with the findings of Franks and Bossert, 1983; see section 3.1.4). This is because the probability of landing on a young (bad) and an old (good) patch must be equal at equilibrium.

The mean and variance of colony size are simply functions of $m$, the size of the daughter colonies, and the mean and variance of patch age depend simply upon the equilibrium population size.

When expressed as the number of births (or deaths) per colony per time step then colony turnover rates simply depend on $m$; the lower the maximum size at which colonies reproduce ($2m$), the faster the colonies turn-over (and presumably the faster the population would recover from any perturbation). A population on a small island (small $K$) with slow patch recovery (large $n$ and hence low $x^*$) and large colony fission thresholds (large $2m$) would therefore be very susceptible to extinction.

### 4.3.3 Spatial models

Britton also developed spatial versions of his model so that he could more closely approximate the J and S versions of the Grid model. The equations were more complicated for the following reason. In the non-spatial model, the probability

of a colony returning to a patch that it exploited in the previous time step was identical to the probability of it raiding any other unoccupied patch on the island. In other words, the patch a colony occupied at time $t+1$ was completely independent of the patch it occupied at time $t$. It can be shown that the probability, $P$, of a colony returning to a patch that it has previously occupied and that has not had time to recover is, in the non-spatial model, given by $P = 1 - (1 - 1/K)^n$. Thus $P$ is about 1.5% if $n = 6$ and $K = 400$. In the non-spatial model it was actually assumed that this was negligible and could therefore be discounted. That this was a reasonable assumption will become apparent soon. However, for the J and S versions of the Grid model, the spatial restrictions to colony movement meant that the patch a colony occupied at time $t+1$ *did* now depend on the patch occupied at time $t$. This in turn meant higher values of $P$, which could not therefore be ignored, thereby making the equations more complicated.

The greater complexity of the equations meant that, apart from those for the mean and variance of the colony size (which remained unchanged; see equations 4.3 and 4.4 above), exact solutions for them could not be found. Equation 4.7 above for the turnover rates still held, but only as an approximation. Numerical approximations to the other formulae have been made, however, for the parameter values $K = 400$, $n = 6$ and $m = 5$. Table 4.3 below shows the predictions made by all three of Britton's models for these particular parameter values.

**Table 4.3** A comparison of the predictions made by Britton's three analytical models (for $K = 400$; $n = 6$; $m = 5$).

| Variables | Analytical Model | | |
|---|---|---|---|
| | Non-spatial Model | Spatial Models J Model | S Model |
| No. of colonies: | 37.7 | 36.6 | 29.2 |
| No. of young patches: | 200 | 191 | 147 |
| Colony size — mean: | 5 | 5 | 5 |
| Colony size — variance: | 4 | 4 | 4 |
| Patch age — mean: | 9.61 | 10.3 | 15.6 |
| Patch age — variance: | 102 | 119 | 273 |
| No. of births per time step = No. of deaths per time step: | 0.754 | 0.732 | 0.585 |

Comparison of Table 4.3 with Tables 4.1 and 4.2 shows that Britton's J and S models agree reasonably closely with my J and S simulation results (especially when allowing for the possibility of multiple patch occupancy in the simulation models; see section 4.3.6a also). Table 4.3 therefore also confirms the four points noted above (in section 4.2.3) about the changes that occurred in passing from the J to the S model. These changes can be explained by the corresponding increase in the likelihood of a patch being re-raided by the colony that just raided it before the patch has had time to recover from the previous raid. Colonies in the S model spent more time raiding through young patches and therefore did not grow as well as those in the J model. Colonies and young patches were therefore rarer in the S model, and mean patch age was higher as a result. When expressed in terms of numbers of births or

deaths per colony, however, turnover rates were the same in Britton's J and S models: the absolute turnover rates were only lower in the S model because of the fewer colonies.

By far the most interesting thing about Table 4.3, however, is the closer fit of the J model to the non-spatial model than to the S model. This finding can be interpreted in a narrow sense and a broad sense. In the narrow sense the result suggests that the probability, $P$, of a patch being re-raided by the same colony that just raided it, and before it has recovered from the previous raid, is almost the same in the non-spatial and J models, whereas it is much higher in the S model. In fact, this probability was about 21% in Britton's S model but only about 4% in the J model, compared to the non-spatial model in which it was assumed to be zero. This last assumption now seems reasonable because although a colony in the non-spatial model could raid patches at a distance less than, as well as equal to, or greater than three patches away, it was much more likely to do the latter on islands of large size (eg., $K$ = 400 patches) relative to the J jump distance of three patches.

But what is the meaning of this finding in the broad sense? Once the average distance between successive statary phase bivouacs exceeds a relatively small value (roughly equivalent to the three step size jumps of the J model), then the probability of a patch being re-raided by the same colony before the patch has recovered is so low that the population dynamics resembles that of a system in which the colonies can jump anywhere at random. Thus, in the broad

sense, space can be omitted from a model of the population dynamics of army ants without losing much explanatory power. In a nutshell, the army ant colonies move through space in such a way that the temporal changes, the raiding and recovery of the patches, matter much more than the spatial affects resulting from the fine details of their movement patterns.

### 4.3.4 Comparison of the non-spatial model with reality

How does Britton's simplest, non-spatial model compare with reality? First the relevant parameter values ($K$, $n$ and $m$) for BCI must be found.

Section 4.2.1 showed that each patch represented an area of 31,684m$^2$. Since BCI has an area of 15.6 km$^2$, the number of patches on BCI is $(15.6 \times 10^6) / (3.1684 \times 10^4) = 492.4$ or about 500. The social insect prey take about 200 days or 200/35 = 5.71 or about 6 time steps to recover from a raid by *E. burchelli*; thus $n = 6$. If colony size is divided into 10 classes, with $2m$ being equivalent to the maximum size of 600,000 workers, and $m$ to 300,000 workers for the daughter colonies, then each size unit represents 600,000/10 = 60,000 workers; $m = 5$.

Inserting $K = 500$, $n = 6$ and $m = 5$ into equations 4.1 to 4.7 above yielded the following predictions for BCI at equilibrium:

1) Number of colonies = $500[1 - (1/2)^{1/(6+1)}] = 47.1$ ($x^* = 47.1/500 = 0.09428$).

2) Number of young patches = 500/2 = 250, or half the island, an area of 15.6/2 = 7.8 $km^2$.

3) Colony size: mean = 5 (ie., 300,000 workers); variance = $(5^2-1)/6$ = 4 (ie., 240,000 $workers^2$).

4) Patch age: mean = (1 - 0.09428)/0.09428 = 9.61 (ie., 9.61 x 35 = 336 days); variance = 9.61/0.09428 = 101.90 (ie., 101.90 x 35 = 3567 $days^2$).

5) Number of births per time step = number of deaths per time step = 500 x 0.09428 / (2 x $5^2$) = 0.9428 (ie., 0.9428 x 365/35 = 9.8 births and 9.8 deaths per year).

Table 4.4 below lists these predictions against the observations for BCI. One third of the 50 or so colonies on BCI reproducing each year is equivalent to (50/3) x (35/365) = 1.60 births and 1.60 deaths per 35 day time step. In reality the actual percentage of colonies reproducing each year on BCI may be less than this because the observations may have been biased towards conspicuous large colonies that are more likely to split.

The model highlights how little is known about the army ant system, particularly in respect of patch ages, but it predicts the equilibrium population size quite well. How sensitive are the models predictions, though, to variations in the parameters? Recall from section 4.3.2 that, once above 4, say, the value of *n* could vary within broad bounds without substantially affecting the estimate of population

**Table 4.4** A comparison of the predictions made by Britton's non-spatial analytical model (for $K$ = 500; $n$ = 6; $m$ = 5) with the observations for BCI.

| Variables | Non-spatial model | Observations for BCI |
|---|---|---|
| No. of colonies: | 47.1 | 45-55 |
| No. of young patches: | 250 | ? |
| colony size[1] mean: | 300,000 workers | ? |
| colony size[1] variance: | 240,000 workers$^2$ | ? |
| patch age mean: | 336 days | ? |
| patch age variance: | 3567 days$^2$ | ? |
| No. of births per time step = No. of deaths per time step: | 0.94 | 1.60 |

**Note:**
1. Rettenmeyer (1963a:369-370) estimated *E. burchelli* colonies to have in the range of 150,000 to 700,000 workers; and Franks (1980:57, 1985) estimated colonies to range in size from 280,000 to 650,000, with an average of about 400,000 workers (n = 7; all sampled in the dry season of 1979). See section 3.1.3d in the last chapter also.

size. However, the model's predictions are quite sensitive to variations in $K$ and $m$. These will be considered in turn.

The value of $K$ depends critically on how a patch is defined. An upper bound to an estimate of the actual 'virgin' area raided during a statary phase can be obtained by assuming that none of the thirteen 89m by 6m raids overlap with each other; yielding a value of 13 x 6m x 89m = 6,942m$^2$. A patch of this size would result in a $K$ value (and hence a predicted population size) over 4.5 times greater than the value used above based on a patch size of 31,684m$^2$. However, it is reasonable to assume that the impact of an army ant raid extends at least a few metres

beyond the swarming army ants themselves, since the zone peripheral to a raid path presumably provides the bulk of the prey that re-invade the area. Since the 13 statary raids are spaced out somewhat like the spokes of a wheel it may be assumed that the raids also affect the areas between the 'spokes' and so a patch size approximately defined by the circumference of such a wheel can be justified.

The parameter *m* is involved in estimating the turnover rates and the mean and variance of colony size. A gain in size of one unit is equivalent to a not unrealistic net increase of 60,000 workers. A fall in one size unit would also mean a net loss of 60,000 workers but an actual loss of 120,000 workers, since an equivalent of the 60,000 new callows must also be lost. Is this a realistic loss when expressed as workers lost per square metre? Total area raided during the statary phase and nomadic phase in a 35 day cycle = (13 x 6m x 89m) + (14 x 6m x 116m) = 6,942$m^2$ + 9,744$m^2$ = 16,686$m^2$. Thus a net loss of 120,000 workers over one cycle is equivalent to an average loss of 120,000 / 16,686$m^2$ = 7.2 workers per square metre. I shall assume this figure is a reasonable upper limit to average mortality or loss of workers from an army ant raid.

Returning to Table 4.4, although the rest of the model's predictions either agree with the observations, or, where the latter are absent or based on poor sample sizes, are not unreasonable, the model clearly underestimates the turnover rates by a factor of almost two.

### 4.3.5 Increasing the turnover rates

How can the model be altered to raise the predicted turnover rates to more realistic values without affecting the other, more satisfactory predictions? To answer this question it was decided to work with the J version rather than the non-spatial version for several reasons. First, the J version is the most biologically realistic compared to the non-spatial and S versions; second, I had written a J version (but not a non-spatial version) of the Grid model for the computer, which could therefore be compared with Britton's predictions; and, third, as was seen in section 4.3.3. above, there was little difference between the results of the non-spatial and J versions of Britton's model in any case.

Using the J version of my Grid model, three different approaches were taken to try to increase the turnover rates without affecting the other predictions of the model. These approaches were: the introduction of a third, 'ancient', patch type; the imposition of colony senescence; and the confining of reproduction to the dry season. Britton, with his J model, was able to verify the findings of the first two of these approaches, and he also had time to investigate the effects of minimum viable colony sizes greater than one.

#### a. Ancient patches

The concept of ancient patches was introduced not only to try to increase turnover rates but also to try to explain an experiment involving Orchid Island. Franks (1982a,c) had

transferred a colony of *E. burchelli* to Orchid Island north of BCI (see Fig. 3.2) to see how a colony would fare in a habitat from which army ants had been excluded for a long time. Franks found that the colony workers sustained high levels of mortality and injuries and showed that the colony was gradually shrinking in size. He attributed this to combat with the defending social insect prey (see also section 2.3.2), which formed a greater proportion of the colony's diet on Orchid than BCI, and which had reached higher densities and larger colony sizes in the absence of predation by army ants.

Thus, although 'old' patches in which the social insect prey have just recovered from an army ant raid may be beneficial to *E. burchelli*, 'ancient' patches, ones in which the social insect prey have had time to reach very high densities, may be harmful. If true, this effectively means that the army ant population is subject to an Allée effect (Allée, 1931; cited in Begon *et al.*, 1986): if the population falls below a certain threshold density, it will decline to extinction (in this case, because of the increasing abundance of ancient patches). In this scenario army ant colonies can only persist if their prey are continually weakened and prevented enough time to build up their defences. This is partly achieved by the presence of other army ants (not necessarily of the same species) raiding through areas and resetting the process of succession whilst a given colony is absent from those areas.

The Allée effect, if it exists, has obvious implications for the conservation of army ants. Any attempt to introduce a species of army ant to an area from which army ants with similar dietary preferences have been absent for some time is only likely to be successful if many army ant colonies are introduced simultaneously. In practice, repeated introductions would probably have to be made.

Returning to the simulation model, the J version was altered so that patches that reached $n'$ time steps in age ($n' > n$) changed from old to ancient and caused colonies that raided them to lose one size unit (as for young patches). Simulations were then run to observe the effects of different values of $n'$ on the dynamics.

**Results**

If $n'$ was large ($n' > 140$ time steps, say) then few if any ancient patches were present on the island at equilibrium and they therefore had very little effect on the equilibrium population dynamics. If $n'$ was small (not much bigger than $n$), however, then old patches became too sparse and ancient patches too abundant to prevent the population from going extinct. If $n'$ fell between these extremes (eg., $n' = 40$) then the population persisted but both the equilibrium population size and the turnover rates were reduced compared to the regular two-patch model. (Interestingly, the number of 'bad' young and ancient patches combined approximately equalled the number of young patches alone at equilibrium in the two patch model. Thus in both models the equilibrium

probabilities of landing on bad and good patches were approximately the same.) Although the following situation was not modelled I suspect that if the magnitude of the impact caused by individual ancient patches was increased still further (eg., to 2 size units), then the results would have been similar to a reduction in $n'$.

Thus it seems ancient patches cannot be used to raise turnover rates without also affecting the equilibrium population size. Britton discovered the same effects when he incorporated ancient patches into his J model. A large value of $n'$ ($n' > 140$), however, is still useful in explaining the Orchid Island experiment without upsetting the predictions for BCI. The Allée effect and the important implications this has for conservation have already been mentioned.

**b. Colony senescence**

Real *E. burchelli* queens apparently live for a maximum of about 6 years (approximately sixty 35 day cycles; see section 3.3.7 in chapter 3). If colonies do not rear a new queen before their current brood has matured they apparently disintegrate (or fuse with another colony). In reality, sexual broods are only reared during the dry season, so unless colonies forestall the potentially disastrous loss of a senescent queen in the wet season by replacing her in the preceding dry season, the colony may disappear as an independent entity. Otherwise, barring accident, the colony as an entity is effectively immortal.

To see just how important queen mortality could be in the extreme I made the simplifying assumption that colonies died when their queens died; no colony fusion was permitted. The original two-patch J model was therefore altered so that colonies died after $L$ time steps. Colonies were assigned a random age at the start of a simulation.

**Results**

Using a value of $L$ equal to 60 (corresponding to a six year lifespan) hardly affected the predictions of the basic J model. This agreed with Britton's results. To raise the turnover rates to more realistic levels $L$ had to be reduced to an unrealistically low value (of 20 time steps at the most; corresponding to a two year lifespan). Low $L$ values also produced lower equilibrium population sizes (just as in the BCI model; see section 3.3.7 of chapter 3) and higher average colony sizes. Interestingly, for $L$ = 60 time steps, almost 30% of all deaths occurred due to 'senescence' rather than to the raiding of a run of bad patches. Britton found an even higher value in his model: 44% mortality due to senescence. (This discrepancy could be a result of the lower turnover rates in Britton's original J model compared to my original J model; compare Tables 4.1 and 4.3.) So even though queen mortality may not affect the turnover rates in reality that does not mean that it is not a significant cause of colony mortality.

Britton was also able to estimate the expected lifetime of a colony at equilibrium in his original J model, in which

queens were effectively immortal and colonies could only die by running through a series of bad patches. The expected lifetime was $2m^2$, or 50 time steps (nearly five years) when $m = 5$. If it is assumed that the average lifespan of a queen is about six years or about 60 time steps, then this result confirms the previous result (in section 3.3.5) that colonies were slightly more prone to die due to a run of bad patches than due to loss of their queen.

Finally, I suspect that a model combining both senescence and fusion would produce high turnover rates without lowering the equilibrium population size. This is because the fusion of a queenless colony with a queenright one would result in a large single colony that would be much more likely to reproduce, thereby replacing the colony that just lost its status as a separate entity. However, I did not have time to explore the affects of fusion.

**c. <u>Seasonal reproduction</u>**

The model year could be roughly divided into ten 35 day activity cycles and the model colonies only permitted to reproduce during the first four of them (roughly corresponding to the 130 day dry season on BCI). As before, only colonies that were at least $2m$ size units could reproduce. Because reproduction was now restricted to the dry season a colony (that was size $2m-1$ by the end of the previous dry season) could conceivably reach a maximum size of $2m+6$ size units. (If the parent colony's size was an odd number, the total size was shared between the two daughter

colonies as evenly as possible.) Reconciling this with the observed maximum colony size of around 600,000 workers meant that the threshold size for fission could be lowered and the turnover rates thereby hopefully increased (recall from equation 4.7 that a low *m* means higher turnover rates).

**Results**

Seasonal reproduction resulted in 'sawtooth'-shaped annual cycles in population size and average colony size (the latter peaking at the end of the wet season), with births and population size peaking at the beginning of the dry season. No pattern in the occurrence of deaths throughout the year could be discerned.

Reducing the minimum size requirement for a colony to reproduce in the dry season, $2m$, had no affects on equilibrium population size, number of young patches, or the average patch age, but it did raise the turnover rates. Not surprisingly, lowering *m* also reduced both the maximum and the average colony sizes. A value of $2m$ of 7 or 8 yielded turnover rates of 1.4 or 1.1 per time step (closer to the figure of 1.6 observed on BCI; see Table 4.4), average colony sizes of 4.0 and 4.5, and maximum colony sizes of 12 or 13 respectively. These maximum colony sizes arose at frequencies equivalent to less than one in about 100 years of observation, and even a maximum size of 13 units (equivalent to 13 x 60,000 = 780,000 workers) is not outrageous.

Unfortunately, Britton did not incorporate seasonal reproduction into his J model because of the complexity involved in having to deal with two different sets of equations, one for each season. However, he did find that reducing *m* in his original J model increased the turnover rates without affecting the population size at equilibrium, just as it did with my model (and also with the BCI model; see section 3.3.4 in the last chapter), albeit with seasonal reproduction.

**d. Greater minimum viable colony sizes**

So far in this chapter, colonies have been allowed to occupy a size range of one to ten units, and colonies that fell to zero size units died. Britton raised the minimum viable size from one up to two units, equivalent to 120,000 workers, roughly corresponding to the smallest colony size quoted by Rettenmeyer (1963a:369) of 150,000 workers. Britton found that the turnover rates in his J model increased by almost 20%, although equilibrium population size was hardly affected.

**e. Summary of attempts to raise the turnover rates**

Seasonal reproduction successfully explained the high turnover rates observed and left virtually unchanged the other predictions of the original J model (see Table 4.1). Ancient patches could be readily incorporated into the model to explain the results of the Orchid Island experiment without compromising the predictions for BCI. Conversely,

if future introductions to Orchid Island showed that the result of Franks's experiment was atypical, then ancient patches could be jettisoned from the model without affecting the predictions for BCI. The extent of colony mortality following queen mortality in nature is unknown, but at least the effects it would have on the dynamics were it found to be prevalent can be predicted. Finally, raising the minimal viable colony size also resulted in higher turnover rates. The extent to which this contributes to the high turnover rates observed in nature awaits more accurate data on minimum viable colony sizes. In short, the J version of the model with both seasonal reproduction and ancient patches, and possibly also larger minimum viable colony sizes, explains many of the observations.

#### 4.3.6 Further considerations

This section addresses some of the criticisms that may be levelled at the very simple models presented in this chapter. The effects of relaxing some of the assumptions (such as only allowing a maximum of one colony in a patch) and of incorporating some extra factors (such as pheromone trail avoidance) will be considered.

**a. Multiple occupation of patches**

Section 4.3.2 showed that my Grid models permitted more than one colony to occupy a patch, whereas Britton's models did not. Comparison of Britton's results (Table 4.3) to mine (Tables 4.1 and 4.2) showed very little differences,

suggesting the affects of multiple patch occupation to be minor. Britton checked this on his J model by allowing for multiple patch occupancy and found that the equilibrium number of colonies (and hence also turnover rates) were very slightly increased. This presumably explains why these two variables had higher values in Table 4.1 than for the J model in Table 4.3. That the affect of multiple occupation of patches is small is simply due to the small chance of more than one colony occupying a patch on a large island.

**b. Pheromone trail avoidance**

If *E. burchelli* colonies really do avoid the pheromone trails of other colonies then patches that have been recently raided are effectively protected from re-raiding until either the pheromone trail has evaporated beyond detectability or until it is at a concentration that does not deter other colonies of army ants. The importance of this effect depends, to a large extent, on the length of time the pheromone trail takes to decay compared to the time it takes for the social insect prey to recover.

The pheromone trail decay time is unlikely to be much more than 35 days (equivalent to one time step; see also sections 3.2.1 and 3.3.3 in the last chapter). Therefore an upper limit to the affect of pheromone trail avoidance on the population dynamics can be gauged by preventing the model colonies from entering any patch less than two time steps old. Britton did this with his J model, and found that the equilibrium number of colonies and number of young

patches were both increased by about 10%. This was because the patches that were one time step old were inaccessible to colonies, thereby resulting in a lower probability of a patch being re-raided before it had recovered from a previous raid by the same colony. Consequently, colonies fared better and they reproduced to produce more colonies which, in turn, raised the number of young patches until a new equilibrium was established.

c. Asynchronous colony activity cycles

In the models of this chapter all the colonies' activity cycles were in total synchrony with each other. In reality, however, colonies of *E. burchelli* appear to be independent of one another with regard to their activity cycles since they exhibit 'all possible differences in phase' from one another (Schneirla, 1949:66). How would the models' results have been affected if colonies were randomly distributed with respect to their activity cycles? This question can be answered by imagining what would happen if none of the colonies were in synchrony with any of the other colonies.

Then, when the time came for any one of these colonies to move, the patches occupied by all the other colonies would be inaccessible to it. This situation is analogous to the trail pheromone avoidance situation considered in the previous section when the colonies are all in perfect synchrony with each other and the pheromone takes one time step to decay. The only difference between the two situations is whether a colony cannot enter a particular

patch because it is occupied by another colony rather than the pheromone trail of another colony. In both cases, the equilibrium number of colonies and young patches would be increased by about 10%. In reality, some colonies will be in synchrony simply by chance and therefore the increases resulting from asynchrony will be somewhat less than 10%.

**d. Edge affects**

None of the models presented here employed true edges. A boundary will effectively confine a colony's movements more to a particular spatial region. This means that a patch near an edge will probably be more likely to be re-raided by the same colony that just raided it before it has recovered from the previous raid. Thus the incorporation of edges into the model would probably have results similar to the conversion of the J to the S model: a reduction in population size (see Table 4.3). The importance of the edge affect obviously depends on the edge:area ratio and hence the size and shape of the island in question. Compared to a given island, a smaller island of the same shape, or another island of the same area but with longer boundaries, will support smaller populations. These conclusions conform with commonly held principles for the design of nature reserves containing populations that are unlikely to be reinforced by immigration across the boundaries and/or which are unsuited to the habitats characteristic of the edges (Diamond and May (1981) and Simberloff (1988) discuss the principles of

reserve design in general, whereas Lovejoy *et al.* (1986) consider the design of reserves for army ants specifically).

### 4.4 Conclusions of the entire modelling exercise

This section brings the work of this and the previous chapter to a close by drawing together what has been learnt from the various modelling approaches about the population dynamics of *E. burchelli* on BCI.

The value of the BCI model was already explained in section 3.4.1 of the last chapter. In this chapter, a series of models was developed in which the statary phase, rather than the nomadic phase, was assumed to be the most important phase in relation to the population dynamics of the army ants. The fairly close fit between the predictions of this model and data from the field suggest that this assumption is valid. The basic model only required three parameters, and, with the incorporation of seasonal reproduction, could also account for the high turnover rates observed. The seasonal model suggested that there are annual cycles in population size; and ancient patches, if important in the real system, could have important implications for any efforts at conservation.

In terms of future research on army ants in the field, an important lesson can be learnt from the modelling exercise in this chapter. It is that the fine details of the movement patterns of *E. burchelli* are relatively unimportant when it comes to explaining their population dynamics. The models revealed that the distance moved

between their statary phase bivouacs is so large that the chances of re-raiding a patch before it has recovered is negligible and little different from a system in which colonies would have no restrictions to their movement. The modelling work indicates that if people wish to know more about army ant population dynamics then field research should place less emphasis on the conspicuous and spectacular colony movement patterns. Rather, future research should focus on first, losses of army ant workers in patches of different ages and from colonies of different sizes, and second, on the relationship between raiding success and the recruitment of workers.

The models also revealed an important, and perhaps counter-intuitive, principle. It might be thought that a larger, and hence more viable, population could be supported on an island if the distance moved between exploited patches was small compared to patch size. However, the comparison of the S and J models showed the exact reverse to be true: larger populations were supported in the same area if the distance between the patches successively exploited by a colony was *large* compared to patch size. Increased distance between exploited patches reduces the chance of a patch being re-raided by the same colony before it has recovered from the previous raid. However, as island size decreases, the probability of raiding a patch before it has recovered will gradually become so high that the distance moved between patches will be virtually irrelevant.

The last paragraph provides a possible evolutionary explanation for why the successive statary phase raid rosettes of *E. burchelli* army ants are three times further apart than they could be. Putting the costs of increased travelling distances to one side, individual colonies (and hence their genes) are more likely to survive and reproduce if they set their statary phase bivouacs further apart, and the population as a whole is more likely to persist as a result. Other things remaining equal, however, it would seem unlikely that the distances would increase much further over evolutionary time because of the negligible gains to be had from further reductions in the already very small probability of re-raiding a patch before it has recovered.

Finally, the various models could, in principle, be adapted and applied to other species of army ants and other geographical areas, and, in a wider sense, possibly even to the foraging and growth strategies of plants and fungi. For other attempts to analyse the latter systems, see, for example, Lovett-Doust and Lovett-Doust (1982) and Sutherland and Stillman (1988) in the case of plants; and Rayner and Franks (1987) in the case of fungi.

# Chapter 5

## An Ecological Field Survey of the Ant *Leptothorax tuberointerruptus*

### 5.1 Introduction

This chapter reports the preliminary results of a 16 month ecological survey of a species of ant found on the south coast of England. The results unexpectedly revealed the probable occurrence of seasonal polydomy (see later). The possible reasons for the origin and maintenance of this phenomenon, and its implications for the study of this species, are discussed at the close of this chapter.

Workers of the European ant *Leptothorax tuberointerruptus* are small, no more than 5mm in length, and the colonies themselves are small, usually with fewer than 500 workers and but a single queen. At certain sites along the south coast of England the nests occur in great density (more than one per square metre) where they typically inhabit crevices in friable rocks. These rocks are easily split open and the ants readily collected. Many colonies can be housed in a relatively small area within the laboratory.

*L. tuberointerruptus* has only been studied in connection with nest-building behaviour (Franks *et al.*, 1992) and the phylogeny of the Leptothoracini tribe (Douwes and Stille, 1987, 1991). Nothing has been published about its ecology. Its abundant colonies, small worker size, small colony size, relatively simple social structure (ie.,

but a single queen) and ease of housing in the laboratory, all contribute to making this species an ideal candidate for an extensive population survey spread over many months. The aim of the survey was to describe, and, if possible, explain, the year round fluctuations in colony size and queen number, and thus to provide baseline ecological data for the use of other ecologists and behaviourists working on this and similar Leptothoracine species.

### 5.1.1 The study species

#### a. Taxonomy

The ant tribe Leptothoracini belongs to the sub-family Myrmicinae (Hymenoptera: Formicidae), but the taxonomy of the tribe itself is confused and currently undergoing revision (Buschinger, 1987; Heinze, 1987; Douwes and Stille, 1987, 1991). The generally accepted scheme proposed by Buschinger (1987) has the Leptothoracini divided into two groups: the '*Leptothorax* group' and the '*Myrafant* group'. *Leptothorax tuberointerruptus* (F.) belongs to the latter group. The species is morphologically similar to, and apparently hybridizes with, several other species in the so-called '*Leptothorax tuberum*' group within the Myrafants: *L. tuberum*, *L. interruptus*, *L. nigriceps*, and *L. unifasciatus* (Douwes and Stille, 1991). However, the latter two species have not been recorded in Britain, whilst *L. interruptus* appears to nest under stones or in heather roots and is restricted to various heathlands (Bolton and Collingwood, 1975). What has been identified as *L. tuberum*

in England and Wales (Bolton and Collingwood, 1975) is almost certainly *L. tuberointerruptus* in all cases (P. Douwes, pers. comm., on the basis of allozyme data). Finally, my study species is strictly called *L. "tubero-interruptus"* (Douwes and Stille, 1991), but, if it is to be used as a proper name, it should be written without the hyphen as *L. tuberointerruptus* (B. Bolton, pers. comm.; P. Douwes, pers. comm.).

**b. Geographical range**

*L. tuberointerruptus* has been recorded below 1000m altitude in France, northern Spain and Italy, and east Germany (P. Douwes, pers. comm.). In Britain, the species has been recorded on or near the coast in most of the southern counties: from Cornwall to the south of Essex, and north to Gloucester and Glamorgan (Bolton and Collingwood, 1975). *L. tuberointerruptus* is therefore near the northern edge of its range on the south coast of Britain.

**c. Habitat**

Nests of *L. tuberointerruptus* on mainland Europe are most often found inside dead twigs either on the ground or still attached to bushes or small trees (Douwes, pers. comm.). However, I and others in England have only ever found its nests in rock crevices or, rarely, in the soil under rocks that are no more than 1 cm in thickness, or in moss growing on a rock. This difference may be due to the absence of competition from other species such as *L. unifasciatus* and

*L. nigriceps* in England (Douwes, pers. comm.; see also Yamaguchi, 1992, for an example of competition for nest sites involving a leptothoracine).

Of the only other two Myrafant species found in Britain, the heathland habitat of *L. interruptus* has already been mentioned, and *L. nylanderi* is only found inland in south England, living under bark or in tree stumps (Bolton and Collingwood, 1975). The species *Leptothorax acervorum* (belonging to the '*Leptothorax* group') also occurs in southern Britain but has larger workers and also nests in association with wood. Thus, on the south coast of England, *L. tuberointerruptus* appears to live in the absence of any interspecific competition for nest-sites in rock crevices, either with other Leptothoracines, or, by virtue of its small size in contrast to the workers of most other species, with other co-occurring species of ants (eg., *Lasius niger*, *Lasius flavus* and *Myrmica scabrinodis*).

**d. Diet**

In the field (Portland Bill, Dorset), I and colleagues have observed single foragers or pairs of foragers of *L. tuberointerruptus* carrying small dead insects, a mite, and a dead *Lasius flavus* worker. Other workers have been seen around the remains of *Myrmica scabrinodis* workers. Remains of *Lasius flavus* and *M. scabrinodis* have occasionally been found in the nests of *L. tuberointerruptus*. Thus *L. tuberointerruptus* appears to scavenge or prey upon small arthropods, including ants (the latter are probably

scavenged rather than killed). In the laboratory *L. tuberointerruptus* will take honey solution and live *Drosophila* larvae.

## 5.2 Methods

### 5.2.1 Collecting site

The nests of *Leptothorax tuberointerruptus* were collected from a limestone grassland site at the top of the western cliffs of Portland Bill, Dorset (NGR SY 680 719). The general location of the site is shown in Fig. 5.1. The site was chosen for its accessibility and abundance of nests. (Note that the term 'nest' is here used in preference to 'colony' since the contents of a single nest may not necessarily represent the entire colony.)

The site was actively quarried until the 1930s at the latest; the biological community is therefore at least 60 years old. The site is characterised by plants typical of a coastal limestone grassland and is virtually devoid of trees. Apart from *L. tuberointerruptus*, the only other species of ants found at the site were, in decreasing order of apparent abundance, *Lasius flavus*, *Lasius niger* and *Myrmica scabrinodis*.

### 5.2.2 Collecting techniques

Fig. 5.2 shows a close-up of the individual collecting sites, the numbers of nests sampled and the 17 dates on which they were collected.

Two people (myself and K.A. Koepke) collected the vast

**Figure 5.1 Map of Portland Bill, Dorset. The rectangular area shows the approximate location of the collecting sites shown in greater detail in Fig. 5.2.**

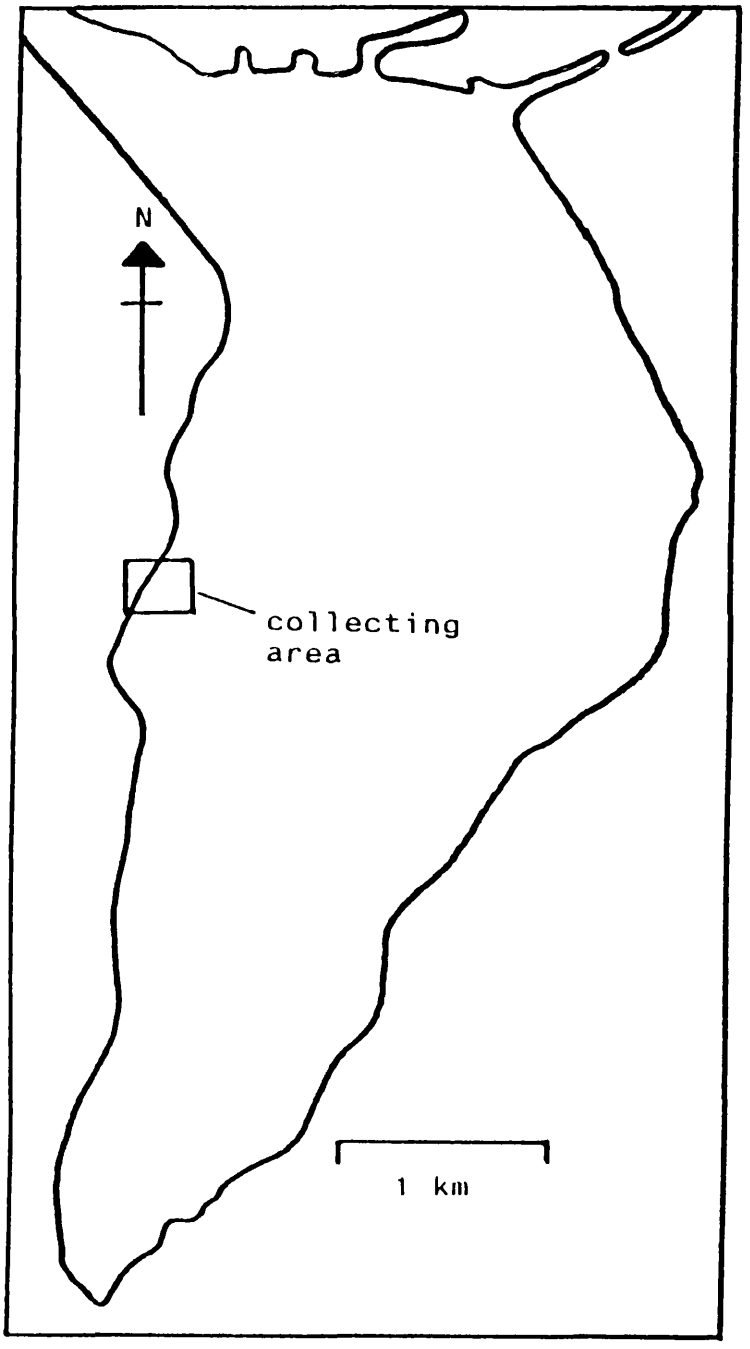


Figure 5.2 Close-up of the collecting area delineated in Fig. 5.1. The numbered areas on the map are the sample sites, and the table shows when the sites were sampled and how many nests were collected.




| Sample date | Sample site(s) | Nest no.s collected | Number of nests collected |
|---|---|---|---|
| 1. 20.02.92 | 1 | 45-57 | 13 |
| 2. 07.03.92 | 1,2 | 58-74 | 17 |
| 3. 26.04.92 | 3,4 | 75-104 | 30 |
| 4. 30.05.92 | 5-10 | 105-135 | 31 |
| 5. 20.06.92 | 11 | 136-165 | 30 |
| 6. 04.07.92 | 12 | 166-195 | 30 |
| 7. 20.07.92 | 13-16 | 196-225 | 30 |
| 8. 08.08.92 | 17 | 226-255 | 30 |
| 9. 29.08.92 | 18 | 256-288 | 33 |
| 10. 17.09.92 | 19 | 289-318 | 30 |
| 11. 22.10.92 | 20 | 319-348 | 30 |
| 12. 21.11.92 | 21 | 349-378 | 30 |
| 13. 15.12.92 | 22 | 379-408 | 30 |
| 14. 17.01.93 | 23 | 409-438 | 30 |
| 15. 20.02.93 | 24 | 439-469 | 31 |
| 16. 27.03.93 | 25 | 470-499 | 30 |
| 17. 01.05.93 | 26 | 500-529 | 30 |

majority of the nests (instead of K.A. Koepke, N.R. Franks and G.M. Orledge collected some on 20.2.92 and 15.12.92 respectively). Although the areas selected were not systematically searched, the searching on each date was restricted to as small an area as possible (see Fig. 5.2). With the exception of site #1 (see Fig. 5.2), a site that had been searched previously was never resampled at a later date. However, the entire sampling effort over the 16 month period was deliberately restricted to as small an area as possible so as to minimise the chances of sampling from more than one population. The nests of *L. tuberointerruptus* were found within or between the friable rocks (which were mainly oolitic limestone) scattered throughout the grass. At least 30 colonies (usually 15 each) were collected within about 2 to 4 hours using a knife to split open the rocks and pooters to aspirate the ants into tubes. Once taken, the ants were not returned to the site so as to minimise disturbance of the recovering community.

### 5.2.3 Treatment of the nests following collection

In the laboratory the ants were transferred to separate 10cm x 10cm x 1.9cm square petri dish arenas containing transparent artificial nests. To stop the ants escaping the arenas had lids and their walls were painted with Fluon (PTFE suspension). The artificial nests each comprised two halves of a 54 mm diameter petri dish with one half inverted and dovetailed with the other half (in which an entrance hole was made) to leave a 1mm gap within which the ants

could reside (see Fig. 5.3). This design forced the ants to occupy a monolayer which facilitated counting once they had emigrated into the nest (which they usually did without intervention by me).

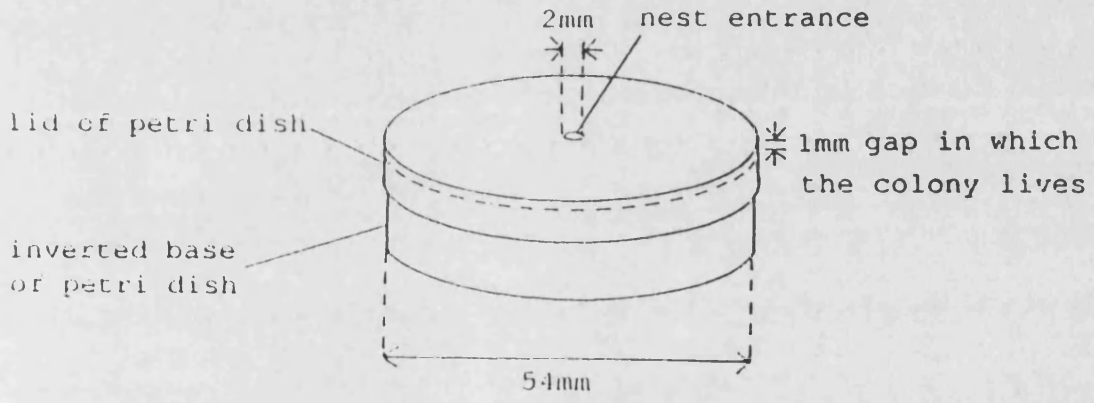
Any male or female sexuals found, either fully winged (alate), or with the visible remains of wings (indicating recent loss of wings, - queens a year or more old have no remaining wing membrane visible, and males never live more than a few days or weeks), were put in petri dishes labelled with their tube number and immediately frozen to -40$^{o}$C for later drying and weighing (see Appendix 3).

The various components of the nest (workers, brood, etc.) were assigned to 12 different categories (see the next section) and counted as follows. The nest was placed over a white background to facilitate the counting of the adults by eye. To count the pale-coloured brood, the nest was placed on a black background and viewed through a dissection microscope at x7 magnification. All counts were made with a manual event counter. Each category was counted twice and the average recorded. For large numbers of items (usually over 100), two successive counts occasionally disagreed by more than 10; counts were repeated in such cases to reduce the discrepancy.

### 5.2.4 Classification of the twelve assigned categories

Most of the 12 categories shown in Appendix 2 are self-explanatory. What were thought to be final instar larvae were classified as 'large larvae'. All remaining larvae

**Figure 5.3 Petri dish nest of the type used to house the *Leptothorax tuberointerruptus* ants.**



recognisable as larvae were classified as 'medium larvae'. If a larva appeared to be on the borderline between these two categories it was assigned to one of them at random. Microlarvae indistinguishable from eggs at x7 magnification were grouped with the eggs into a single category. Prepupae could be distinguished from large larvae as follows. Prepupae were opaque whereas larvae were translucent, and prepupae lacked a meconium (an accumulation of undigested material visible through the body of a larvae as a dark mass, and which is egested by the larva on becoming a prepupa). Male prepupae were occasionally difficult to distinguish from worker prepupae but the former tended to be longer and thinner with a more tapered posterior. In such cases, and if both male and worker prepupae had been positively identified in the same or other nests collected at the same time, the prepupa was assigned to the worker or male categories at random.

### 5.2.5 Treatment of the females

The reproductive status of the females was assessed by behavioural observations, and, in many cases, by dissection of their reproductive tracts. If a nest contained a single dealate (wingless) female which generally remained immobile and surrounded by workers among the younger brood items, then that female was assumed to be a mated egg-layer and the mother of the workers. If, however, the lone female was quite active and worker-like in its behaviour (carrying brood or nest material, venturing outside the nest, etc.)

its reproductive tract was dissected to determine (a) if it was mated, and (b), if it was an egg-layer. In any case, a female was dissected if, on rare occasions, her reproductive status was questionable on the basis of her behaviour. If a nest contained more than one dealate female that were not obviously sexuals (see section 5.2.3) then all the dealates were dissected.

The dissection details will not be elaborated here. It is only important to know that although it was relatively easy to tell whether or not a female had been mated (merely by inspection of her spermatheca) it was not always clear whether or not a female had laid eggs. Like the workers themselves in *L. tuberointerruptus* (pers. obs.), virgin females still have the potential to lay viable haploid eggs that can develop into males. It is most unlikely that *L. tuberointerruptus* workers can produce diploid offspring because no spermathecas were found in the few workers I dissected, and Alloway *et al.* (1982) also found no spermathecas in the workers of any of three closely related Myrafant species.

## 5.3 Results

The raw data are shown in Appendix 2 for all 12 categories on all 17 dates sampled. The sexual dry weight data are shown in Appendix 3. Most of these data have only been included for the sake of completeness and for the benefit of other researchers requiring ready access to my data. My purpose here, however, is to concentrate only on the

demography of worker and queen numbers throughout the year. Correct interpretation of these data provides an essential foundation for the proper understanding of other phenomena, such as the allocation of resources to growth versus reproduction, or to male versus female sexuals (see section 5.4.5).

Virtually all statistical tests were performed using the mainframe computer package 'Minitab' (Release 7.2; Minitab Inc., Pennsylvania, USA). If any tests were not supported by Minitab I implemented them as C computer programs using the relevant formulae from Sokal and Rohlf (1981).

### 5.3.1 Comparison of the collectors' results

On the eleven sampling dates from 20.7.92 to 1.5.93 the identity of the collector was recorded on the tube into which each nest was pooted (see Appendix 2). Before the results can be interpreted biologically the data for the two collectors should be compared to see if they were biased with respect to each other. For instance, one of the collectors might have been more prone to overlooking queens; any patterns in queen number might therefore have simply reflected the relative numbers of nests collected by the two people rather than any real biological phenomenon. The data were therefore grouped into four simple categories: brood, workers, males and females (the latter comprised all females, whether mated or unmated, alate or dealate). These categories were chosen to reflect what could easily be resolved by the naked eye during the few minutes it took to

collect each nest. Only if there are no significant differences in the numbers collected by the two people is it possible to be reasonably certain that the two people were not biased with respect to each other and that their data can be pooled into a single sample. It does not follow from such results, however, that the two collectors were not biased with respect to reality (eg., they could both have been overlooking queens with equal frequency). Even if such biases do occur, however, variations and trends in the data should still be revealed.

Table 5.1 summarises the results of the comparisons for each of the four categories. On ten of the dates, the collectors were K.A. Koepke and myself; on the eleventh (15.12.92), they were G.M. Orledge and myself.

The results in Table 5.1 show that there were no significant differences between the two collectors for any of the four categories. Henceforth, the results for both collectors will be pooled into a single data set and the results for all 12 categories will be treated as if a single collector had taken all the nests. It is further assumed that all the data gathered before 20.7.92 can be treated as if they were collected by a single person.

### 5.3.2 Numbers of mated females

Fig. 5.4 shows the number of mean mated females (assumed to be the maternal queens of the workers in the nest) per nest over the sampling period 28.2.92 to 1.5.93. Note that the data for the 13 and 17 nests collected on 20.2.92 and 7.3.92

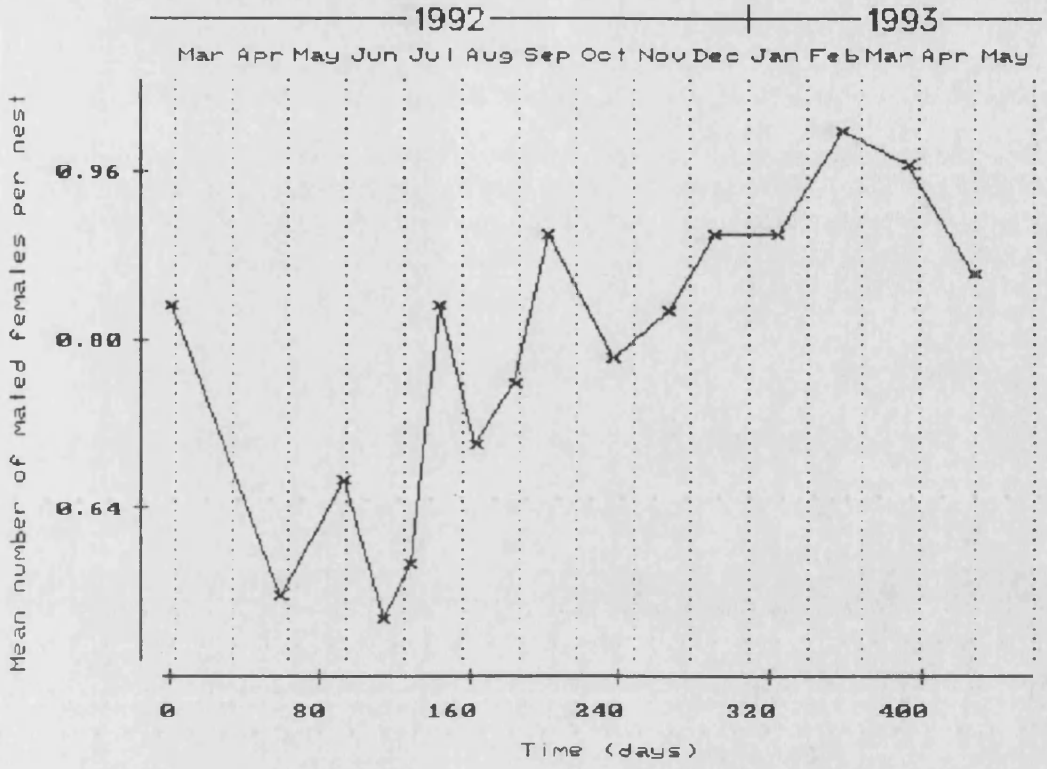
**Table 5.1 Comparison of the numbers of brood, workers, males and females collected by K.A. Koepke (KAK) and myself (LWP), and by G.M. Orledge (GMO) and myself.**

| Category | KAK & LWP (10 dates) | GMO & LWP (15.12.92 only) |
|---|---|---|
| Brood | 1) Friedman's test on the means: S = 13.2; df = 9; P = 0.16 (NS)<br>2) 10 Mann-Whitney U-tests: no significant results at the 5% level. | One-way anova: F = 0.23; df = 1, 28; P = 0.64 (NS) |
| Workers | 1) S = 14.4; df = 9; P = 0.11 (NS)<br>2) No significant Mann-Whitney test results. | F = 0.39; df = 1, 28; P = 0.54 (NS) |
| Males | One-way anova on the $\log_{10}(X+1)$ transformed data for 20.7.92: F = 0.05; df = 1, 28; P = 0.83 (NS) | (No males were found on 15.12.92.) |
| Females | 1) S = 13.1 (adjusted for ties); df = 9; P = 0.16 (NS)<br>2) No significant Mann-Whitney test results. | $\text{Log}_{10}(X+1)$ transformed formed data: F = 0.91; df = 1, 28; P = 0.35 (NS) |

**Note:** Three types of statistical test were performed: Friedman's test (a non-parametric alternative to the two-way anova), using only the mean results of each collector for each date; repeated Mann-Whitney U-tests on all the data for each of the dates in turn; and, finally, one-way anova (analysis of variance). df = degrees of freedom. Of the 11 dates, males were only found on 20.7.92. Unless stated otherwise, all tests were performed on the raw untransformed data. (NS = test result not significant, P > 0.05.)

respectively were not significantly different for any of the categories then recorded (see Table 5.2). In all following analyses these two data-sets have therefore been pooled to yield a sample of 30 nests 'collected' on the average date

**Figure 5.4 Mean number of mated females per nest as a function of time.**




of 28.2.92 (making a total of 16 dates over which sampling occurred).

**Table 5.2 One-way anova results for the comparison of the mean numbers of brood (only eggs and larvae were found), workers and queens collected on 20th Feb. and 7th Mar. 1992 (All F values had 1 and 28 df; 'NS' - test result not significant, P > 0.05).**

| Category | F | P | Significance |
|---|---|---|---|
| Brood | 0.24 | 0.63 | NS |
| Workers | 1.29 | 0.27 | NS |
| Queens | 0.05 | 0.83 | NS |

Fig. 5.4 shows that the average number of mated females in a nest varied between about 0.5 and 1.0. Generally a nest contained only one mated queen or no queen at all. If there was more than one queen, usually only one had been mated, although the rest were apparently capable of laying unfertilized eggs that could develop into males. Out of a total of 484 nests sampled between 20.2.92 and 1.5.93, only 9, or 1.9%, definitely had two mated queens (the queens of one other nest were suspected of being mated but the dissection results were ambiguous). In such cases the queens fought each other, aggressive acts were observed among the workers, and some workers would attack the queens; one of the queens would usually be killed within a few days or weeks of collection. These cases probably represented two independent nests in close proximity in the field that were accidentally collected together. Laboratory experiments in which two queenright nests were placed together also resulted in the death of one of the queens. Thus we can assume that *Leptothorax tuberointerruptus* is monogynous; ie, only one mated queen is allowed to lay diploid eggs (which develop into workers or females; haploid eggs develop into males).

The reproductive status of the queens in 14 of the 484 nests sampled was indeterminate for various reasons. Of the remaining 470 nests, 108 were queenless and 362 queenright (353 with one mated queen, plus 9 with two mated queens). Remember that 'queenless' merely refers to the absence of any females that have been mated; a 'queenless' nest may

still have had one or more virgin females capable of laying haploid eggs that could develop into males. A chi-squared test showed that there was a highly significant association between the number of queens per nest and the sampling date ($chi^2$ = 41.2; df = (2-1)x(16-1) = 15; P < 0.001). The dates could be split into two groups: (A), the 4 dates from 26.4.92 to 4.7.92, and (B), the 12 dates of 28.2.92 and 20.7.92 to 1.5.93 (but see section 5.4.6). Within both of these groups there was no significant association between queen number and date. Table 5.3, however, shows that group A had many more queenless than queenright nests, whilst group B had many more queenright nests than expected by chance under the null hypothesis of there being no association between queen number and date.

**Table 5.3 Contingency table showing the observed numbers of queenless and queenright nests in the two sampling periods A and B (defined in the text). Shown in parentheses are the numbers of nests expected under the null hypothesis of there being no association between queen number and date. $Chi^2$ = 29.5 on 1 df; P << 0.001.**

| | | Number of queens per nest: Zero | 1 or 2 | Total |
|---|---|---|---|---|
| Date Group | A | 48 (26.7) | 68 (89.3) | 116 |
| | B | 60 (81.3) | 294 (272.7) | 354 |
| | Total | 108 | 362 | 470 |

In sum, for most of the sample period from 28.2.92 to 1.5.93, about 83% (294 out of 354) of the nests had mated

queens, but this dropped very significantly to only 59% (68 out of 116) in the period from late April to early July 1992.

### 5.3.3 Numbers of workers overlooked during collection

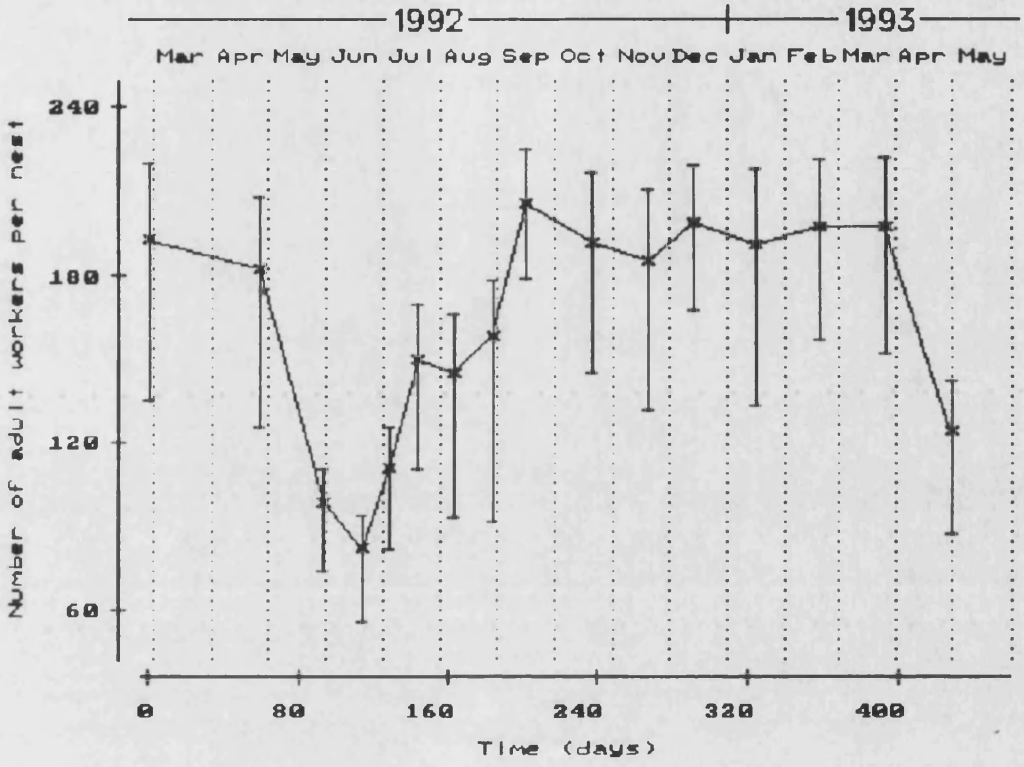
Before considering worker numbers in detail, the amount of sampling error attached to the results will be briefly examined. On 1.5.93 (the last collection made), G.M. Orledge returned to 15 of the nests 50 to 60 minutes after they had been sampled by K.A. Koepke and myself to see how many workers we might have overlooked in our initial collections (the data I report in this thesis do not include Orledge's data on the extra workers). Such workers either escaped during the process of collection, or were not in the vicinity of the nest during collection (the workers might have been foraging, or in transit from a neighbouring nest for example).

The number of extra workers Orledge found ranged from 3 to 40, with a mean of 21.3 (s.d. = 12.25; n = 15). If these numbers are included with the numbers collected by Koepke and myself, then they account for anywhere between 3.5% and 27.6% of the total workforce (mean = 14.7%; s.d. = 6.70%).

### 5.3.4 Variation in nest size through time: queenless and queenright nests combined

Fig. 5.5 shows the mean number of workers per nest throughout the whole sample period. The trough in numbers in May to July 1992 (and the apparent beginning of one in

**Figure 5.5 Mean numbers of workers against time in all (queenless and queenright) nests combined. The bars represent the 95% confidence limits for each mean. The confidence limits are asymmetrical because they were backtransformed from the square-root transformed data.**




April-May 1993) is distinctive, but tests need to be done to see whether or not it is statistically significant.

Of the 16 distributions of worker numbers, only the distribution corresponding to the sample date of 4.7.92 is significantly different from a normal distribution (in fact, it is slightly skewed to the right). If the raw data are square-rooted, however, all 16 distributions then become not significantly different from normal (ie., the transformed data have a high correlation with their normal scores). Their variances are heterogeneous, however (Hartley's $F_{max}$-

test: $F_{max}$ = 6.14; 16 samples; df = 29; P < 0.01; see Sokal and Rohlf, 1981:403), meaning that the analysis of variance cannot be used here. The non-parametric equivalent to the one-way anova, the Kruskal-Wallis test, shows that the worker numbers differ very significantly on at least two of the dates (H = 93.7 adjusted for ties; df = 29; P < 0.001). Sokal and Rohlf (1981:408) recommend the Games and Howell method as an approximate test for the equality of means when the variances are heterogeneous. When this method was applied to the transformed data, many of the means turned out not to be significantly different from one another and could be pooled to form new groups. Eventually, it was found that the 16 means could be simplified into just two groups within each of which the means were not significantly different. In one group, representing the 12 sampling dates of 28.2.92 to 26.4.92 and 20.7.92 to 27.3.93, the mean number of workers per nest was 182.7 (s.d. = 92.5; n = 363 nests). In the other group, representing the 4 sampling dates of 30.5.92 to 4.7.92 and 1.5.93, the mean number of workers was only 103.9 (s.d. = 62.4; n = 121). The difference between these two groups was highly significant (Mann-Whitney U-test: W = 18111.5 adjusted for ties; P < 0.0001).

Thus, in early May to early July (pooling those dates for 1992 and 1993), the average size of nests fell to only about 57% of the size that they had been (ie., of approximately 183 workers) for the rest of the sampling period. The trough in worker numbers is statistically

highly significant and appears to be a regular phenomenon in the late spring to early summer.

### 5.3.5 Variation in nest size through time: queenless and queenright nests considered separately and then compared

Worker numbers in queenless and queenright nests over all 16 dates were analysed by two-way anova, with queen status and sample date as the two main factors. The anova was a 'mixed model' design (Sokal and Rohlf, 1981:322) in which date was treated as the random (Model II) factor and queen status as the fixed (Model I) factor. This was because it was already known that nest size varied through time (see the previous section) and I therefore had no intention of comparing the different dates. In contrast, however, queenless and queenright nests were to be compared, and queen status was therefore treated as a fixed treatment, even though the queen status for each nest collected had not been under the control of the experimenter (see Sokal and Rohlf, 1981:202-207 for a discussion of Model I and II anovas). Any nests for which the queen status was unknown were omitted from the analysis.

Of the 32 distributions of worker number (ie., two distributions for each of the 16 dates), only three were significantly different from normal: the distributions for the queenless nests on 30.5.92, 8.8.92 and 21.11.92. All three distributions had single outliers with many more workers than the other queenless nests collected at the same time. For the three respective dates these outliers were

nest numbers 109, 243 and 353. The queens had probably been overlooked during the collection of nests 109 and 243, whilst 353 probably comprised two separate colonies accidentally collected in the same tube (since, in the laboratory, many dead workers were found and worker-worker aggression was observed). When these three nests were omitted from the analysis, the distributions for the three dates were no longer significantly different from normal. (Although these nests were not omitted either from the analysis in the previous section or from Fig. 5.5, it is unlikely that their omission would have affected the conclusions very much.)

Table 5.4 shows the results of the two-way anova. Note that the date x queen status interaction mean square (MS) is tested over the error MS. The date MS is also tested over the error MS, but the queen status MS is tested over the interaction MS because the latter is significant (Sokal and Rohlf, 1981:340).

The date x queen status interaction term is significant. This means that the relationship between worker number and queen status depends on the date, or, conversely, that the relationship between worker number and date is contingent upon queen status. So how do the sizes of queenless and queenright nests compare on each of the 16 dates in turn? To answer this question 16 planned orthogonal comparisons are required. The term 'planned' refers to the intention to conduct the comparisons before

**Table 5.4 Results table for a mixed model two-way analysis of variance of worker number, with sample date as the random factor and queen status as the fixed factor (nests 109, 243 and 353 have been omitted).**

| Source of variation | degrees of freedom, df | Sum of Squares, SS | Mean Square, MS | F | P |
|---|---|---|---|---|---|
| date | 15 | 308511 | 20567 | 3.69 | P < 0.001 |
| queen status | 1 | 603937 | 603937 | 62.50 | P < 0.001 |
| date x queen status | 15 | 144949 | 9663 | 1.73 | P < 0.05 |
| error | 435 | 2423341 | 5571 | | |
| Total | 466 | 3480738 | | | |

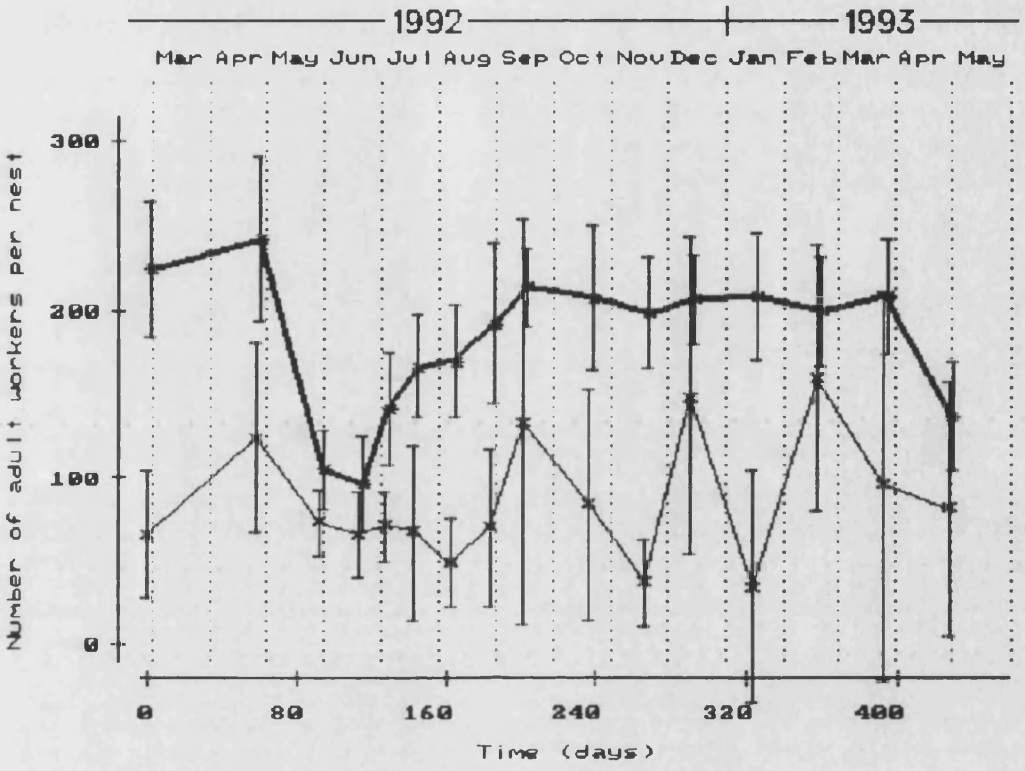
the results of the anova were known (Sokal and Rohlf, 1981:232); the term 'orthogonal' effectively means that the comparisons to be made are independent of one another (see Sokal and Rohlf, 1981:233-241 for a detailed definition and discussion of orthogonality). Table 5.5 shows the results of the 16 comparisons. Since each comparison only involves two groups, there is only one degree of freedom and the MS = SS/df = SS/1 = SS. Each F value in Table 5.5 was obtained simply by dividing the MS of the corresponding comparison by the error MS (= 5571) of the two-way anova of Table 5.4. Thus the F values all have 1 and 435 degrees of freedom.

Fig. 5.6 shows the mean numbers (with 95% confidence limits) of workers in queenless and queenright nests on the same axes for comparison. It shows that queenright nests

**Table 5.5** Planned orthogonal comparisons of the numbers of workers in queenless and queenright nests on the 16 sampling dates. See text for details. P values: NS (not significant) $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. P values are enclosed in parentheses if there were five or fewer queenless nests involved in the comparison.

| Date | No. of queenless nests | No. of queenright nests | MS | F | P |
|---|---|---|---|---|---|
| 28.2.92 | 6 | 24 | 120936 | 21.71 | *** |
| 26.4.92 | 12 | 15 | 93063 | 16.70 | *** |
| 30.5.92 | 9 | 20 | 6537 | 1.17 | NS |
| 20.6.92 | 14 | 16 | 7315 | 1.31 | NS |
| 4.7.92 | 12 | 17 | 35444 | 6.36 | * |
| 20.7.92 | 5 | 25 | 41317 | 7.42 | (**) |
| 8.8.92 | 8 | 21 | 86321 | 15.49 | *** |
| 29.8.92 | 9 | 24 | 98089 | 17.61 | *** |
| 17.9.92 | 3 | 27 | 17893 | 3.21 | (NS) |
| 22.10.92 | 5 | 18 | 59849 | 10.74 | (**) |
| 21.11.92 | 4 | 24 | 89540 | 16.07 | (***) |
| 15.12.92 | 4 | 26 | 11872 | 2.13 | (NS) |
| 17.1.93 | 3 | 27 | 82006 | 14.72 | (***) |
| 20.2.93 | 2 | 28 | 3138 | 0.56 | (NS) |
| 27.3.93 | 3 | 27 | 34206 | 6.14 | (*) |
| 1.5.93 | 6 | 23 | 14884 | 2.67 | NS |
| Totals: | 105 | 362 | | | |

**Figure 5.6 Mean numbers of workers against time in queenright (thick line) and queenless (thin line) nests separately. Nest numbers 109, 243 and 353 are not included. The bars represent the 95% confidence limits for each mean.**




always have more workers, on average, than queenless nests on a given date, although this is not significant on six of the 16 dates (see Table 5.5). Incidentally, if all 105 queenless nests are grouped together and compared with the 362 queenright nests in another group, the difference in worker number is highly significant (MS = 902306; F = 161.96 on 1 and 435 df; P << 0.001). Thus, over all 16 dates, queenright nests had significantly more workers than queenless nests.

Table 5.5 shows that on half of the 16 dates there were five or fewer queenless nests (there were never fewer than

15 queenright nests). The results of comparing the queenless and queenright nests on these eight dates were accordingly susceptible to considerable sampling error. Hence it is not possible to determine whether these P values would remain approximately constant or be completely changed unless and until more queenless nests have been sampled at these times of the year. Until then it is prudent to restrict any biological interpretations to the remaining eight dates on which more than five queenless nests were sampled (see section 5.4.2 below).

## 5.4 Discussion

### 5.4.1 Queen number in *Leptothorax tuberointerruptus*

*L. tuberointerruptus* appears to be monogynous: only one mated female per nest is tolerated, although further, unmated, females are capable of laying eggs that develop into males.

That *L. tuberointerruptus* is monogynous was confirmed by genetic analysis of forty of the nests taken from Portland Bill. Fifteen and 25 of the nests collected on 17.9.92 and 22.10.92 respectively were sent to P. Douwes in Sweden for allozyme analysis (using the techniques described in Douwes and Stille, 1991). He analysed the queens and at least ten workers from each of the nests and found that 37 of the nests had a single mother and probably a single father, two nests had a single mother and probably two fathers, and one nest was probably an accidental collection of three separate colonies (Douwes, pers. comm.). Allowing

for two males being identical by chance at the locus in question, two of the 37 nests probably had two fathers rather than one; and allowing for sampling error (ie., missing one or more of the genotypes among the workers), Douwes also inferred that another four of the remaining 35 nests probably had two fathers as well. Thus 31, or 79%, of the 39 nests had allozyme results consistent with the interpretation of one mother and one father, whilst the remaining eight nests, or 21%, had one mother and two, or possibly more than two, fathers.

Now consider the variation in queen number through time. Not all the nests sampled would have been expected to have queens: some queens may have been overlooked during sampling and also some nests may have been 'orphaned', ie., lost their queen and which, therefore, were presumably senescing through their inability to produce new workers. Such explanations might account for the observation that only 83% of the nests were queenright throughout most of the survey period, but what about the sudden drop to only 59% of the nests having a mated queen in the period 26.4.92 to 4.7.92? A possible explanation for this trough in queen number per nest is postponed until the next section.

### 5.4.2 Worker number in *Leptothorax tuberointerruptus* and the possibility of seasonal polydomy

If the results of 1992 and 1993 are taken together, a striking trough in worker number was apparent from early May to early July. The average nest size during late spring was

only 57% of the value of about 183 workers it held for the rest of the survey period. This trough coincided roughly with the trough in queen number in 1992 (compare Figs 5.4 and 5.5). If attention is confined to those results for the dates on which more than five queenless nests were found (Table 5.5), then no significant difference in nest size was only found between queenless and queenright nests during the period of the trough in worker numbers. For the rest of the sample period, queenright nests were significantly larger than queenless nests (see Fig. 5.6).

The most likely explanation for the temporary and apparently regular annual drops in queen number and worker number is seasonal polydomy: the seasonal fragmentation of a single colony into more than one nest-site, followed by the later recoalescense to a single nest-site. First, though, several alternative hypotheses must be evaluated:

1) The trough in worker number in late spring simply reflected a reduced efficiency of sampling the workers because the proportion of workers away from the nest was greatest during that period. Section 5.3.3 revealed that on 1.5.93 almost as many as 27% of the workers may have been missed in the original collection; if Orledge had waited longer than 50-60 minutes, she may have collected even more workers. First, however, this hypothesis cannot account for the coincident trough in queen number. Second, the weather, and temperature in particular, appeared to influence the activity of the ants and hence their ability to escape collection: the ants were much more active and harder to

collect during days of hot weather. Yet cold and hot weather occurred on collection dates both inside and outside the troughs in queen and worker numbers per nest. Sampling error, therefore, would appear to be a poor explanation for the queen and worker troughs (but see section 5.4.6).

2) Many workers a year or more old died in late spring and were replaced by new workers eclosing from pupae shortly afterwards. Data on worker mortality are unfortunately lacking, but worker pupae were found in nests from 30.5.92 to 29.8.92 and eclosion of the 1992 generation of adult workers commenced on 20th June, precisely the time when worker numbers were at their lowest. The last new adult workers to emerge were seen on 17.9.92, arguably the end of the 1992 trough in worker number (see Fig. 5.5). Yet the mean number of workers on 17.9.92 was not significantly different from any other mean in the group of 12 dates mentioned in section 5.3.4: the trough statistically ended on 4.7.92. Thus the rise out of the trough had ended in 1992 when new workers were still emerging: it appears that recruitment of new workers cannot be the major factor contributing to the rise out of the trough. Moreover, apart from the difficulty of seeing why worker numbers should decline at a time when they would apparently most be needed to rear the pupal workers and sexuals to maturity, the hypothesis of worker death followed by recruitment does not explain the trough in queen numbers.

3) The demographic phenomena are a result of nest reproduction by fission, followed by nest growth (rather as

in army ants). Suppose a large queenright nest fragments to produce a second nest nearby with worker and sexual brood but no queen. This would account for both the decline in worker numbers per nest and in the proportion of queenright nests. Then, so the hypothesis would run, one of the daughter queens mates and takes over the new nest. Finally, both the parent and daughter nests grow rapidly (and hence rise out of the trough in worker numbers) since they both have many workers and many worker pupae compared to a colony founded by a single queen after a mating flight. This hypothesis is untenable for many reasons. First, the allozyme results of Douwes suggested that the single mated queen in each nest was, in every case, the mother and not the sister of the workers. If the hypothesis was true, then at least some of the queens would have been expected to be the sisters of the workers, at least whilst the initial workers were still alive. Second, for a daughter queen to take over the new nest she would either have to go on a nuptial flight during or after which she mated with a male, or she would have to exhibit pheromonal 'sexual calling' behaviour to attract potential mates to her nest. However, in the first case it seems unlikely that the female could ever relocate her nest after the nuptial flight (see also Franks, Sendova-Franks, Sendova-Vassileva and Vassilev, 1991), and, in laboratory experiments with sexuals, I have never witnessed females of *L. tuberointerruptus* exhibit sexual calling behaviour (see also Buschinger, 1987). Third, if new nests were produced by fission of established

nests, why should so many adult females be produced (one nest on 20.6.92 was found with 65 alate females) if only one can take over the new nest? Army ant colonies reproduce by fission, but produce very few adult females, only one of which takes over the new colony (Franks and Hölldobler, 1987). Fourth, the mean dry weights of the adult females increased very significantly ($P < 0.01$ by the Games and Howell method) over the three dates on which they were sampled (data not reported here). Such a 'fattening up' of the females would be expected for species in which colonies were founded by lone females (eg., *Lasius niger*, Boomsma and Isaaks, 1985): a single female is probably going to depend heavily on her internal food reserves to rear the first batch of workers (Hölldobler and Wilson, 1990:157), even if she does add to her reserves by some risky foraging. Alternatively, there seems to be much less reason for a female to fatten herself up if she will be assisted in the establishment of a new colony by many workers from her parent colony. Indeed, it has been shown that the extent to which the queen is fattened up prior to dispersal is a good indicator of the mode of colony founding (Keller and Passera, 1989; see also Passera and Keller, 1990). Fifth, although very few (less than ten) incipient colonies have been found at Portland Bill (ie., colonies with a queen, some brood and few if any workers), they would be expected to be hard to locate anyway because of their small size. Alloway *et al.* (1982) also found very few incipient colonies and suggested that that was indirect evidence for colony

fission being a frequent means of colony reproduction. However, the three species of Myrafants they were studying were, unlike *L. tuberointerruptus*, facultatively polygynous (ie., sometimes had more than one mated queen per colony) and therefore had a ready source of fertile queens for occupation of any new daughter colony. Thus, if some nests are produced by fission of established nests in *L. tuberointerruptus*, then they can only represent a small proportion of the attempts at colony foundation and certainly could not account for the population-wide troughs in worker and queen number per nest.

Three further lines of evidence are also consistent with the hypothesis of seasonal polydomy:

1) The close proximity (5 to 20cm) of many nests in the field, plus observations in the laboratory that workers from one nest are usually hostile to workers from nests paired up at random with them, suggest that neighbouring nests are either parts of the same colony or, if workers are less aggressive to kin than non-kin, closely related colonies. Occasional collection of neighbouring nests in the same tube also usually revealed no greater worker mortality or aggression than was typical for a single nest of comparable size. One possibility is that neighbouring nests are unrelated but do not recognise each other as 'foreign' because recognition may be based on odour cues obtained from the local environment (Stuart, 1987; see also Stuart, 1988). However, workers from different nests that have been kept in

the same laboratory environment for two months will still fight each other (pers. obs.).

2) When a nest of *L. tuberointerruptus* is disrupted in the laboratory, the entire colony can relocate to a new nest-site within a few hours. On 20.6.92 and 29.6.93 at Portland Bill, workers were observed to carry brood from one nest-site to another; in both cases the emigrations or transits appeared to be spontaneous rather than due to disturbance by the observer. In laboratory experiments a colony forced to emigrate has occasionally fragmented, with parts of the colony moving into different nest sites and remaining there until, in one case, the experiment was terminated over a month later. These observations at least indicate that *L. tuberointerruptus* has the behavioural flexibility required of a seasonally polydomous species.

3) Although not reported here, either no statistically significant differences were found between queenless and queenright nests for many variables that were examined (mainly relating to the production of sexuals), or the pattern of differences varied from date to date in a manner difficult to interpret. The lack of clearly defined and/or consistent differences between the queenless and queenright nests in these statistical tests suggests that the absence of a mated queen in a given nest is not a reliable indicator of queenlessness in the colony as a whole. Many of the queenless and queenright nests are probably simply different parts of the same polydomous colonies.

### 5.4.3 Testing for seasonal polydomy

All three lines of evidence are circumstantial, however, and do not represent critical tests of the hypothesis of seasonal polydomy. How have other researchers inferred the presence of seasonal polydomy?

Polydomy has been reported in several species of ants (see, for example, Levings and Traniello, 1981; Alloway *et al.*, 1982; Del Rio Pesado and Alloway, 1983; MacKay and MacKay, 1983; Rosengren and Pamilo, 1983; Fletcher and Ross, 1985; Stuart, 1985; Herbers, 1984, 1985, 1987, 1991; Herbers and Tucker, 1986; Pollock and Rissing, 1989). Intriguingly, seasonal troughs in worker number concomitant with temporary rises in the numbers of queenless nests were also discovered long ago in two North American species of Myrafant: *Leptothorax longispinosus* (Headley, 1943) and *L. curvispinosus* (Headley, 1943; Talbot, 1957). Research conducted since then has confirmed that both species, together with another co-occurring relative of theirs, *L. ambiguus*, are seasonally polydomous (Alloway *et al.*, 1982; Stuart, 1985; Herbers, 1984, 1985, 1987).

Probably the most intensive study of seasonal polydomy to date, however, is that conducted by Snyder and Herbers (1991) on the North American ant *Myrmica punctiventris*. They inferred the presence of seasonal polydomy from a combination of approaches: seasonal patterns in nest demography (eg., numbers of workers and queens per nest); repeated mapping of the spatial configuration of nests in the field, which allowed them to monitor seasonal changes in

nest density and aggregation patterns, as well as the emigrations, fissions and fusions of nests; worker transfer experiments to assess the responses of workers in a nest to workers from other nests at varying distances away; allozyme analysis to assess the genetic similarity of different nests; and, finally, casual behavioural observations of workers moving alone or carrying brood or adult nestmates between established nests during the season of greatest activity.

To assess whether seasonal polydomy is definitely occurring in *Leptothorax tuberointerruptus*, I would recommend the following approaches:

1) Changes in nest density and spatial aggregation patterns should be monitored throughout the year. If seasonal polydomy was occurring then the period of greatest nest density and aggregation would be expected to coincide with the period of lowest worker and queen numbers per nest.

2) If possible, direct behavioural observations of nest dynamics in the field should be made (perhaps involving the marking of workers to distinguish separate nests): can nests actually be *observed* to fission in late spring and recoalesce in summer? In the manner of Alloway *et al.* (1982) and Herbers and Tucker (1986), the spatial arrangement of nests in the field could be duplicated using artificial nests in the laboratory to follow the fates of ants collected from the field. Colonies could be provided with extra nest sites to see if they will fission and then recoalesce at a later date (eg., see Stuart, 1985).

3) The genetic relatedness of neighbouring nests should be examined. If neighbouring nests really do belong to the same colony then all the workers should be daughters of the same queen.

4) The proportion of queenless nests with healthy, diploid brood (ie., potential adult workers or queens) should be examined. Diploid brood can only be produced by a mated queen (see section 5.2.5), so if a queenless nest is found with diploid brood, then either the queen has died within the last few months or year (unlikely if many of the diploid brood are very young), or the queen is alive but in another nest of the same colony and workers have simply transferred some of her brood to the nest in question. This assumes the queen has not been overlooked during collection. Queenless nests with only male brood almost certainly represent senescent nests with egg-laying workers rearing male reproductives.

### 5.4.4 Possible reasons for the existence of seasonal polydomy

If it is granted that *L. tuberointerruptus* is seasonally polydomous, then why might seasonal polydomy have evolved? Why does *L. tuberointerruptus* exhibit seasonal polydomy rather than permanent monodomy or permanent polydomy? None of the following hypotheses are mutually exclusive, and the selective pressures or other factors responsible for the origin of seasonal polydomy are not necessarily the same as those responsible for maintaining it today (Gould and

Lewontin, 1979). Also, once seasonal polydomy has arisen, it may in turn provide a platform for further evolutionary changes, some of which may contribute to or oppose the maintenance of seasonal polydomy.

Hypotheses based on the advantages of seasonal polydomy fall into four main categories:

1) Risk spreading strategies (see also Rosengren and Pamilo, 1983): eg., spreading the colony over several sites reduces the chance of the whole colony being destroyed should one of the nest subunits succumb to disease or predation (eg., see Droual, 1984). (These reasons are similar to those given by Hölldobler and Wilson, 1977, for why many species of ants have more than one functional queen.) Partly related to this is the hypothesis that different stages of brood should be separated from each other to reduce the chances of cannibalism.

2) Efficient resource exploitation: temporary fragmentation may bring with it the temporary advantages of monopolisation of a greater foraging area, a form of local resource enhancement (Rosengren and Pamilo, 1983). Further, the distances that must be travelled between food sources and the brood may be reduced (MacKay and MacKay, 1983).

3) Colony ergonomics: if maximum colony growth rates can only be achieved within a limited range of colony sizes (Oster and Wilson, 1978; but see also Cole, 1984), then polydomy might allow a nest that would otherwise exceed this size range to fragment into smaller nest units with combined growth rates higher than the original nest (see also Stuart,

1987). Stuart (1985) did not measure growth rates in the facultatively polydomous and North American Myrafant species *Leptothorax curvispinosus*, but he did find that larger nests were significantly more likely to become polydomous than smaller ones. Seasonal polydomy might alternatively provide a means of exploiting extra nest space only when the colony requires it, namely when it is rearing many sexuals and new workers through to maturity. The rest of the time it is more efficient and, in some respects, probably safer for the colony to remain intact at a single nest site. Alternatively, if different types of brood (eg., males versus females) have different optimal growth requirements, polydomy may allow the separation of these brood types into different sub-units (Stuart, 1985), each with their peculiar microclimate most favourable to that particular type of brood. The same may be true for the final maturation of the adult sexuals, although, if applicable to *L. tuberointerruptus*, the distribution of the sexuals among the nests did not in any way seem to correlate with the queen status of a particular nest (see the end of section 5.4.2 above).

4) Reproductive strategies or conflicts: for instance, polydomy may allow a subset of the workers to evade the queen and allocate resources to male and female reproductives in a way that enhances their own fitness rather than that of the queen (Fletcher and Ross, 1985; Stuart, 1985; Herbers, 1990; Snyder and Herbers, 1991); or perhaps to rear their own males rather than the sons of the

queen. Finally, polydomy may be a prelude to colony fission (but see section 5.4.2 above).

The number and diversity of these speculative hypotheses is a strong indication of the lack of data available at present to distinguish among them, but at least they provide pointers for further work. My own opinion runs as follows. The adult members of a colony (and the brood manipulated by the adults) become more active and appear to spread out within the nest as temperatures rise, whereas in winter they are clustered into a single mass (pers. obs.). Combined with the growth of the brood, and the finding that larger brood items are accorded more space than smaller items (Franks and Sendova-Franks, 1992), this expansion of the colony might mean that it will exhaust the available area within its existing nest-site. Recall that the nests are situated within rock crevices which presumably offer little scope for expansion. The colony might then fragment, taking a portion of its brood to another nest-site, thus reducing the crowding among the nest occupants. Workers might shuttle back and forth between the nest-sites carrying brood and nestmates as conditions dictate (eg., one nest-site might become hotter than the other, making it temporarily unsuitable for brood development; many ant species engage in behavioural thermoregulation, moving their brood around in a way that affects their growth and development; Hölldobler and Wilson, 1990:370-374; Porter and Tschinkel, 1993). However, once the adult sexuals have emerged and presumably left their nests on their nuptial

flight, and once the temperatures have begun to fall again, the colony probably recoalesces into a single unit. Winter survival of the ants is presumably directly correlated with the number of ants clustering together (see Hölldobler and Wilson, 1990:373); having all the colony members in one place probably also promotes efficiency of task allocation within the colony and reduces the risk of exposure to predation (mainly from other ants, eg., *Lasius niger* and *Myrmica scabrinodis* at Portland Bill; pers. obs.). Predation by other ants on workers of *L. tuberointerruptus* that are regularly travelling between nest-sites in the season of polydomy could be a major source of mortality. Thus, in my interpretation, polydomy arises simply through the exigiencies of space; once the requirements for space have elapsed with the departure of the sexuals, the costs of polydomy through increased exposure to predation outweigh the benefits, and the various components of the colony recoalesce into a single nest-unit once more. Finally, once seasonal polydomy has arisen then certain parties within the nest may begin to exploit the opportunity, eg., some workers may try to evade the queen and influence the allocation of resources among the sexuals (see the next section also).

### 5.4.5 Implications of seasonal polydomy

If seasonal polydomy really is occurring in *L. tuberointerruptus*, then what are the ramifications of this knowledge for the study of other aspects of this and related species? As far as I know, this is the first European

leptothoracine in which polydomy has been discovered, and it may also be the first obligately monogynous species of ant to be discovered worldwide that is polydomous. Before the survey of *L. tuberointerruptus* was embarked upon it was thought that the species had a relatively simple social structure, namely monodomy (one nest per colony), monogyny (one mated queen per colony), and monoandry (one father per colony). Such a species would be ideal for comparison with species that displayed more complex social structures, such as *Leptothorax longispinosus*, which shows variable amounts of gyny (number of mated egg-laying queens per nest) in addition to facultative polydomy (Herbers, 1986; Herbers and Tucker, 1986). However, it now appears that *L. tuberointerruptus* is facultatively polydomous, although at least it does seem to be monogynous and monoandrous in the main (see section 5.4.1). Moreover, production of males by the workers and possibly also the virgin queens cannot be ruled out (see section 5.2.5).

The previous section alluded to the importance of seasonal polydomy with respect to the study of colony ergonomics, resource exploitation and life-history strategies. However, knowledge of seasonal polydomy is also of great importance in the study of sex allocation, that is, the study of how the parents' or colony's resources are apportioned between the male and female offspring.

Ever since the seminal paper by Trivers and Hare in 1976 sex allocation in social insects has been the subject of intensive study. Using the concept of kin selection,

Trivers and Hare (1976) suggested that, under certain circumstances, one should expect to see a conflict between the workers and queen in the amount of resources invested by the colony in the male and female sexuals. They applied their theory to the ratio of investment at the level of the population, but since then the level of focus has shifted from the population as a whole to the explanation of the variation in investment among colonies within a population (Taylor, 1981; Nonacs, 1986a,b; Frank, 1987; Boomsma and Grafen, 1990, 1991; Pamilo, 1991a,b). For several years it has been realised that polydomy potentially allows groups of workers rearing brood in relative isolation from their queen to manipulate the investment ratios with reduced interference from the queen (Herbers, 1984; Fletcher and Ross, 1985; Snyder and Herbers, 1991). Support for this hypothesis was found in two seasonally polydomous species of North America: *Leptothorax longispinosus* (Herbers, 1984) and *Myrmica punctiventris* (Snyder and Herbers, 1991). In both cases, queenless nests (most of which were interpreted as parts of queenright colonies rather than as orphaned colonies) were found to rear more female biased sex ratios than the queenright nests, in accordance with the predictions of Trivers and Hare (1976). If it had not been known that these two species were seasonally polydomous, then the patterns of sex allocation among the nests would have been difficult to interpret. However, once seasonal polydomy is known to occur it can be used to advantage as a means for testing the affect of the immediate presence or

absence of the queen on sex ratios, whilst automatically controlling for many of the other factors thought to influence sex ratio (listed in Herbers, 1990; see also Snyder and Herbers, 1990). The discovery of seasonal polydomy in *Leptothorax tuberointerruptus* is therefore a crucial aid to the understanding of resource allocation in this species.

**5.4.6 Addendum** (added on 18.1.94)

Two caveats need to be made about the way data were gathered and analysed in this chapter. First, even within a run of random data it is possible to select two sets of points that are statistically significantly different from one another. In section 5.3.2 the data for the numbers of mated females per nest on 1.5.93 should have been included with those for 26.4.92 to 4.7.92 to see if there really was a significant drop in the mean number of mated females per nest between late April and early July. Second, the 26 sample sites shown in Fig. 5.2 were not sampled at random. It therefore becomes difficult to determine whether any trend in the data is a result of spatial or temporal variation. For instance, was the trough in the mean number of mated females per nest shown in Fig. 5.4 a regular seasonal phenomenon (as was intimated in this chapter); or was it merely that the sample sites corresponding to the trough (ie., sites 3 to 12 in Fig. 5.2) were clustered in an area characterised by unusually low numbers of mated females per nest?

# Chapter 6

## Epilogue

Three apparently disparate topics have been explored in this thesis: the application of Lanchester's theory of combat to ants; the population dynamics of army ants; and a demographic study of an ant population on the south coast of Britain. Now that these topics have been addressed in their own light, is it possible to see if they can be united in some way by an underlying theme or general principle?

One such theme is resource allocation. In the case of warfare, how are resources allocated between the competing alternatives of increased individual fighting value and the recruitment or production of more individuals with the same fighting value? In the case of army ants, how are resources allocated between growth and reproduction? Finally, in the case of *Leptothorax tuberointerruptus*, how are the resources of a colony distributed among the available nest sites? An alternative, but related, theme to resource allocation might be the interplay between the size and number of individuals within a society.

However, it is difficult to conceive of a coherent theme that will unite the three topics in such a way that fundamentally deeper insights into the topics will be gained; insights that will generate new predictions. Instead, therefore, it might be more profitable to ask what lessons can be drawn from the three topics for the way

future biological investigations may be conducted. Each of the topics will be considered in turn.

The study of Lanchester's combat theory illustrates the importance of a biologist being prepared to look outside his immediate field of study for any principles that may provide valuable insights. When this happens he should also be alerted to the possibility that such principles can be applied elsewhere (see section 2.7).

The research on army ants has run the whole gamut of simple to complex models, and, in doing so, has encountered the pros and cons of each (see Fig. 3.3). One valuable lesson to be learnt, and which is equally applicable to all models irrespective of their complexity, is that it is absolutely critical to define the aims of a modelling exercise. Definition of the aims assists in the development of the model by providing guidance on which features of reality should be omitted or included, and on the level of detail that is required to model the inclusions (Starfield and Bleloch, 1986); but it also allows the success or otherwise of the model to be evaluated. Without a purpose or goal in mind it is difficult to know what to do next or when to stop. This is probably true of any investigative exercise, but it is often overlooked when bogged down in the intricacies of modelling (Bedford, 1993).

Both of the preceding topics were highly theoretical and used other researchers' data as a starting point. A field study, such as the one performed on *Leptothorax tuberointerruptus*, provides a valuable counterpoint to this

by allowing the biologist to appreciate the problems of gathering and interpreting 'messy' data (missing observations, unequal sample sizes and so forth) typical of ecological studies. Having such experience better equips the biologist to interpret the data of others. For instance, sampling bias was invoked in section 3.3.6 as one of the reasons for the discrepancy between the BCI army ant model's predictions of the average distance between successive statary phase bivouacs and that observed by Willis (1967).

The fieldwork also highlighted the pitfalls associated with generalising from limited sample sets. Had the field sampling been restricted to a short period of the year it might have been assumed that queen numbers and nest sizes remained constant throughout the year, and the possibility of seasonal polydomy consequently overlooked. As was shown in section 5.4.5 of the last chapter, this is a crucial piece of information for the interpretation of such phenomena as sex allocation. It is important to realise that although the field sampling was not limited so much in the temporal sense, it certainly was in the spatial sense: witness the different nesting habitats found at Portland Bill and on mainland Europe (section 5.1.1c). If greater exposure to predation by, or competition with, other ants is indeed an important cost to polydomy (see section 5.4.4), and if such costs are high in some areas of the geographical range of *Leptothorax tuberointerruptus*; then some populations of this species might not be seasonally

polydomous at all, especially if their nest cavities are sufficiently large to contain a mature colony.

To sum up, this thesis work has revealed important lessons regarding receptivity to new ideas; the relative merits of simple and complex models; the importance of setting down the aims of any modelling exercise; the interpretation of biological data as opposed to artificial data generated by models; and finally the perils of extrapolation.

**Acknowledgements**

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For my work on army ant modelling I am especially indebted to the gracious patience and help of Nick Britton; great advances have resulted from our collaboration. Chris Tofts wrote the screen-dump routine for my BCI model and also provided invaluable guidance on the philosophy of modelling.

Kristine Koepke selflessly endured miserable weather to help me collect the nests of *Leptothorax tuberointerruptus*; with her assistance my sample sizes were literally doubled. I am eternally indebted to her. Per Douwes was very kind to analyse the nests I sent him and to put up with my barrage of queries, and Paul Christie provided valuable statistical advice.

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## Appendix 1

### Derivation of equation 2.11

This appendix explains the derivation of equation 2.11 in section 2.2.3 of chapter 2. The equation was given to show the power of the divide-and-conquer strategy in a situation of concentrated attack.

Consider the general situation in which side $m$ divides side $n$ into $k$ equal sized sets of $n_0/k$ combatants each, and then takes on each set in turn with an undivided army according to the dictates of Lanchester's square law. The task here is to show that, when $n = 0$, side $m$ will have the following number of survivors:

$$m = \sqrt{[m_0^2 - (\alpha.n_0^2)/(\beta.k)]} \qquad \text{Eq.(2.11)}$$

Let $M_i$ be the number of survivors on side $m$ after the $i^{th}$ battle. The task, therefore, is to find the number of survivors $m = M_k$ after the $k^{th}$ battle.

Section 2.2.2 showed that if there is only one battle between the two undivided sides (ie., $k = 1$), then, when $n = 0$, side $m$ will have the following number of survivors:

$$m = \sqrt{[m_0^2 - (\alpha/\beta).n_0^2]} \qquad \text{Eq.(2.8)}$$

So, how many survivors will side $m$ have when the first subset of side $n$'s army has been annihilated in a divide-and-conquer situation? The answer is given by replacing $n_0$ in equation 2.8 with $n_0/k$. Then, by the end of the first battle, side $m$ will have the following number of survivors:

$$M_1 = \sqrt{[m_0^2 - (\alpha/\beta).(n_0/k)^2]}$$

These $M_1$ survivors now take on the second of side $n$'s $k$ subsets. Therefore, in addition to the substitution of $n_0/k$ for $n_0$ in equation 2.8, $m_0$ is now replaced by $M_1$. After the second battle, therefore, side $m$ will have $M_2$ survivors:

$$M_2 = \sqrt{[M_1^2 - (\alpha/\beta).(n_0/k)^2]}$$
$$= \sqrt{[[m_0^2 - (\alpha/\beta).(n_0/k)^2] - (\alpha/\beta).(n_0/k)^2]}$$
$$= \sqrt{[m_0^2 - 2(\alpha/\beta).(n_0/k)^2]}$$

Similarly, after the third battle, side $m$ will have $M_3$ survivors:

$$M_3 = \sqrt{[M_2^2 - (\alpha/\beta).(n_0/k)^2]}$$
$$= \sqrt{[[m_0^2 - 2(\alpha/\beta).(n_0/k)^2] - (\alpha/\beta).(n_0/k)^2]}$$
$$= \sqrt{[m_0^2 - 3(\alpha/\beta).(n_0/k)^2]}$$

Thus, in general, after the $i^{th}$ battle ($1 \leq i \leq k$), side $m$ will have $M_i$ survivors:

$$M_i = \sqrt{[m_0^2 - i(\alpha/\beta).(n_0/k)^2]}$$

So, after the last of the $k$ battles, $i = k$, and therefore side $m$ will be left with the following number of survivors:

$$M_k = \sqrt{[m_0^2 - k(\alpha/\beta).(n_0/k)^2]}$$
$$= \sqrt{[m_0^2 - (\alpha.n_0^2)/(\beta.k)]}$$
$$= \text{equation 2.11; QED.}$$

## Appendix 2

### Count data for the *Leptothorax tuberointerruptus* study

This appendix contains the data on the contents of all the nests of *Leptothorax tuberointerruptus* collected from Portland Bill, Dorset. For the first three collection dates (ie., colony numbers 45-104) the brood were not divided into further categories. Thereafter, the categories were counted and defined as in sections 5.2.3 and 5.2.4 of chapter 5. Note that the figures shown here are not the original counts, but the means of the two original counts. The symbol '*' denotes a missing value.

Occasionally (see the appropriate data sets), female/worker intercastes (or 'intermorphs') were found. These were individuals with morphological characteristics and an overall body size intermediate between those of workers and queens. For instance, they were often alate or recently dealate, but their thoraxes were not as large as those of the queens. Nine of the ten intermorphs found were dissected but a spermatheca (which was smaller than that of a queen) was found in only one of them. The intercastes, like the queens, usually had 6 ovarioles (workers usually only have two). All intercastes could probably lay haploid eggs, and some could perhaps be mated and lay diploid eggs too. The intercastes are mentioned where they occurred in the collections below, but they were not included in either the WA or FA totals (nor were they dried and weighed).

The column headings are defined as follows:

COL = identification number of the COLony (or, more specifically, nest).

SA = identification number of the person or SAmpler who collected the nest. This information was only recorded for the 11 dates from 20.7.92 to 1.5.93 inclusive.

0 = Kristine A. Koepke (KAK);

1 = Lucas W. Partridge (LWP);

2 = Guy B. Blanchard (GBB);

3 = Glenda M. Orledge (GMO).

BRD = all BRooD items combined. This category only applies to nests 45-104, and only refers to eggs plus larvae since no prepupae or pupae were found in any of these nests.

EM = Eggs and Microlarvae.

ML = Medium Larvae.

LL = Large Larvae.

WPP = Worker PrePupae.

FPP = Female PrePupae.

MPP = Male PrePupae.

WP = Worker Pupae.

FP = Female Pupae.

MP = Male Pupae.

WA = Worker Adults.

FA = Female Adults (both mated and unmated, alate and dealate).

MO = mated female adults, probably, but not necessarily, the MOthers of the workers. These were not dried and weighed.

VI = unmated female adults (VIrgins). VI = FA - MO.

MA = Male Adults.

EVI = Extra VIrgin female adults (see below).

EMA = Extra Male Adults.

The latter two categories apply only to the collection dates 20.6.92, 4.7.92, 20.7.92 and 29.8.92. EVI and EMA refer to adult male and female sexuals that were not seen (probably because they were still pupae) when the VI and MA were taken a few days earlier for freezing prior to drying and weighing (as described in section 5.2.3 and Appendix 3). The EVI and EMA were seen and counted when the rest of the nest contents were counted on the dates shown with each appropriate data set below. The dry weights and condition of the VI and MA that were weighed are given in Appendix 3. When analysing numbers of sexuals rather than weights of

sexuals, it is recommended that VI be combined with EVI, and MA with EMA, to produce larger and more accurate samples.

The data for the 17 collection dates are on the following pages:

**1) 20 February 1992**

13 nests (numbers 45-57) were collected by LWP and Nigel R. Franks from site 1 (see Fig. 5.2). The nest contents were counted on 25th and 26th February, 1992.

| COL | BRD | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|
| 45 | 282.5 | 310.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 46 | 33.0 | 12.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 47 | 65.5 | 38.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 48 | 56.0 | 72.5 | 1.0 | 0.0 | 1.0 | 0.0 |
| 49 | 110.0 | 85.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 50 | 114.0 | 130.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 51 | 192.5 | 149.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 52 | 342.5 | 395.5 | 2.0 | 2.0 | 0.0 | 0.0 |
| 53 | 225.5 | 183.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 54 | 110.0 | 93.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 55 | 184.5 | 197.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 56 | 170.5 | 212.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 57 | 397.5 | 299.0 | 1.0 | 1.0 | 0.0 | 0.0 |

**2) 7 March 1992**

17 nests (numbers 58-74) were collected by LWP and KAK from sites 1 and 2. The nest contents were counted on 13th and 14th March, 1992.

| COL | BRD | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|
| 58 | 42.5 | 31.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 59 | 35.0 | 88.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 60 | 11.5 | 66.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 61 | 104.5 | 111.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 62 | 158.0 | 196.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 63 | 283.5 | 225.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 64 | 188.5 | 203.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 65 | 198.5 | 202.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 66 | 267.0 | 294.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 67 | 184.5 | 238.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 68 | 89.5 | 267.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 69 | 274.5 | 237.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 70 | 191.5 | 256.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 71 | 58.5 | 171.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 72 | 242.0 | 302.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 73 | 109.5 | 276.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 74 | 243.0 | 435.5 | 1.0 | 1.0 | 0.0 | 0.0 |

**3) 26 April 1992**

30 nests (numbers 75-104) were collected by LWP and KAK from sites 3 and 4. The nest contents were counted between 28th and 30th April, 1992, inclusive.

| COL | BRD | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|
| 75 | 122.5 | 158.5 | 1.0 | * | * | 0.0 |
| 76 | 322.0 | 273.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 77 | 228.0 | 417.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 78 | 185.0 | 292.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 79 | 137.0 | 235.0 | 5.0 | 0.0 | 5.0 | 0.0 |
| 80 | 159.0 | 206.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 81 | 48.5 | 36.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 82 | 76.0 | 83.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 83 | 103.0 | 89.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 84 | 20.0 | 63.5 | 1.0 | * | * | 0.0 |
| 85 | 190.5 | 240.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 86 | 23.0 | 82.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 87 | 197.0 | 140.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 88 | 114.5 | 94.0 | 10.0 | 1.0 | 9.0 | 0.0 |
| 89 | 193.5 | 169.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 90 | 0.0 | 9.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 91 | 328.5 | 275.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 92 | 191.5 | 160.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 93 | 82.0 | 244.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 94 | 58.5 | 104.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 95 | 284.0 | 306.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 96 | 257.0 | 346.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 97 | 172.0 | 297.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 98 | 166.5 | 194.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 99 | 77.0 | 119.0 | 2.0 | * | * | 0.0 |
| 100 | 152.0 | 84.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 101 | 16.0 | 25.5 | 1.0 | 0.0 | 1.0 | 0.0 |
| 102 | 190.5 | 244.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 103 | 216.5 | 249.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 104 | 147.0 | 219.5 | 1.0 | 1.0 | 0.0 | 0.0 |

**4) 30 May 1992**

31 nests (numbers 105-135) were collected by LWP and KAK from sites 5 to 10 inclusive. The nest contents were counted between 3rd and 5th June, 1992, inclusive.

| COL | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 105 | 22.5 | 119.0 | 33.0 | 32.0 | 0.0 | 2.0 | 20.0 | 0.0 | 35.0 | 112.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 106 | 9.5 | 68.5 | 26.5 | 28.0 | 0.0 | 0.0 | 8.0 | 0.0 | 0.0 | 78.0 | 1.0 | * | * | 0.0 |
| 107 | 0.0 | 51.5 | 6.0 | 3.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 35.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 108 | 11.5 | 53.0 | 23.5 | 18.0 | 0.0 | 1.0 | 3.0 | 13.0 | 6.0 | 93.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 109 | 3.0 | 55.5 | 35.0 | 19.5 | 5.0 | 41.5 | 0.0 | 0.0 | 3.0 | 202.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 110 | 24.5 | 28.5 | 13.0 | 6.0 | 6.0 | 5.0 | 0.0 | 19.5 | 23.0 | 205.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 111 | 27.5 | 33.5 | 4.0 | 2.0 | 0.0 | 2.0 | 0.0 | 1.0 | 0.0 | 73.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 112 | 18.0 | 62.0 | 21.0 | 20.0 | 0.0 | 0.0 | 12.0 | 0.0 | 0.0 | 62.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 113 | 4.0 | 30.5 | 3.0 | 3.0 | 0.0 | 15.0 | 6.0 | 3.0 | 80.0 | 74.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 114 | 37.0 | 90.0 | 17.0 | 17.5 | 0.0 | 5.0 | 0.0 | 3.0 | 2.0 | 93.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 115 | 16.5 | 63.5 | 27.5 | 46.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 65.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 116 | 16.5 | 62.5 | 16.5 | 26.5 | 0.0 | 0.0 | 9.0 | 0.0 | 0.0 | 31.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 117 | 15.5 | 3.0 | 0.0 | 2.0 | 7.0 | 5.0 | 0.0 | 17.0 | 12.0 | 83.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 118 | 51.0 | 50.5 | 7.0 | 14.5 | 30.5 | 18.5 | 6.0 | 4.0 | 27.0 | 139.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 119 | 21.0 | 95.0 | 26.5 | 27.5 | 0.0 | 16.5 | 0.0 | 0.0 | 0.0 | 168.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 120 | 24.5 | 66.5 | 2.0 | 3.0 | 19.0 | 0.0 | 0.0 | 29.0 | 0.0 | 156.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 121 | 19.5 | 143.0 | 14.5 | 2.0 | 0.0 | 5.0 | 0.0 | 2.0 | 0.0 | 102.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 122 | 28.5 | 184.0 | 20.5 | 96.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 | 99.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 123 | 20.0 | 60.0 | 12.5 | 39.0 | 6.0 | 12.5 | 0.0 | 20.0 | 3.0 | 177.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 124 | 16.5 | 70.5 | 15.0 | 18.0 | 0.0 | 0.0 | 12.0 | 0.0 | 0.0 | 46.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 125 | 39.0 | 46.0 | 11.5 | 19.0 | 6.0 | 0.0 | 5.0 | 21.0 | 7.0 | 113.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 126 | 26.0 | 66.5 | 33.5 | 14.5 | 0.0 | 9.0 | 1.0 | 0.0 | 0.0 | 109.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 127 | 45.0 | 102.0 | 26.0 | 15.0 | 6.0 | 28.0 | 0.0 | 0.0 | 0.0 | 166.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 128 | 7.5 | 44.0 | 11.0 | 12.0 | 3.0 | 19.5 | 0.0 | 1.0 | 8.0 | 104.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 129 | 6.0 | 82.0 | 25.0 | 21.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 71.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 130 | 26.5 | 21.5 | 11.0 | 24.0 | 1.0 | 2.0 | 0.0 | 43.5 | 10.0 | 110.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 131 | 2.0 | 9.0 | 5.0 | 3.0 | 9.0 | 0.0 | 0.0 | 10.0 | 6.0 | 62.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 132 | 0.0 | 50.5 | 17.5 | 15.0 | 0.0 | 1.0 | 1.0 | 0.0 | 0.0 | 49.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 133 | 27.5 | 12.5 | 8.5 | 3.0 | 2.0 | 3.0 | 0.0 | 9.0 | 16.0 | 54.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 134 | 7.0 | 20.0 | 10.0 | 80.0 | 0.0 | 8.5 | 0.0 | 0.0 | 0.0 | 92.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 135 | 2.0 | 8.0 | 3.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 10.0 | 1.0 | 1.0 | 0.0 | 0.0 |

**5) <u>20 June 1992</u>**

30 nests (numbers 136-165) were collected by LWP and KAK from site 11. The VI and MA sexuals were counted and frozen on 22nd and 23rd June, 1992. The rest of the categories (including EVI and EMA) were counted between 24th and 26th June, 1992, inclusive.

| COL | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA | EVI | EMA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 136 | 7.0 | 23.5 | 4.5 | 32.0 | 0.0 | 1.0 | 73.0 | 23.0 | 1.0 | 74.0 | 16.0 | 0.0 | 16.0 | 4.0 | 2.0 | 1.0 |
| 137 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 19.0 | 0.0 | 0.0 | 9.0 | 0.0 | 0.0 | 0.0 | 11.0 | 0.0 | 1.0 |
| 138 | 1.0 | 8.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 29.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 139 | 20.5 | 46.5 | 14.5 | 17.5 | 0.0 | 6.0 | 85.0 | 0.0 | 38.0 | 75.0 | 1.0 | 1.0 | 0.0 | 3.0 | 0.0 | 9.0 |
| 140 | 28.5 | 17.0 | 0.0 | 7.0 | 0.0 | 1.0 | 66.0 | 0.0 | 0.0 | 19.0 | 1.0 | 1.0 | 0.0 | 2.0 | 0.0 | 1.0 |
| 141 | 14.5 | 137.5 | 9.5 | 6.0 | 0.0 | 6.0 | 69.0 | 0.0 | 13.0 | 93.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 142 | 17.0 | 112.0 | 3.0 | 24.0 | 0.0 | 1.0 | 106.0 | 0.0 | 5.0 | 154.5 | 24.0 | 1.0 | 23.0 | 48.0 | 2.0 | 24.0 |
| 143 | 16.0 | 45.5 | 4.0 | 15.0 | 0.0 | 3.0 | 41.0 | 10.0 | 3.0 | 66.0 | 16.0 | 1.0 | 15.0 | 2.0 | 4.0 | 2.0 |
| 144 | 14.5 | 41.5 | 2.0 | 13.5 | 0.0 | 0.0 | 51.0 | 0.0 | 7.0 | 150.5 | 24.0 | 1.0 | 23.0 | 79.0 | 2.0 | 26.0 |
| 145 | 10.5 | 66.5 | 5.0 | 47.0 | 0.0 | 4.0 | 152.5 | 17.0 | 5.0 | 130.0 | 26.0 | 0.0 | 26.0 | 0.0 | 15.0 | 4.0 |
| 146 | 19.0 | 37.5 | 21.0 | 34.5 | 0.0 | 0.0 | 64.0 | 24.0 | 52.0 | 156.5 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 3.0 |
| 147 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 32.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 |
| 148 | 50.5 | 39.5 | 4.0 | 7.0 | 0.0 | 0.0 | 57.0 | 0.0 | 0.0 | 193.5 | 29.0 | 1.0 | 28.0 | 41.0 | 2.0 | 66.0 |
| 149 | 4.0 | 79.5 | 6.0 | 7.5 | 0.0 | 5.5 | 10.0 | 4.0 | 57.0 | 46.0 | 10.0 | 0.0 | 10.0 | 0.0 | 6.0 | 3.0 |
| 150 | 0.0 | 66.5 | 15.0 | 39.5 | 0.0 | 1.0 | 45.0 | 33.0 | 18.0 | 100.5 | 15.0 | 1.0 | 14.0 | 5.0 | 0.0 | 15.0 |
| 151 | 2.0 | 13.0 | 8.0 | 10.0 | 0.0 | 11.5 | 45.5 | 26.0 | 38.0 | 68.0 | 1.0 | 1.0 | 0.0 | 1.0 | 1.0 | 3.0 |
| 152 | 28.5 | 102.0 | 7.5 | 17.0 | 0.0 | 2.0 | 92.0 | 13.0 | 15.0 | 88.5 | 2.0 | 1.0 | 1.0 | 0.0 | 50.0 | 0.0 |
| 153 | 8.5 | 45.5 | 5.0 | 12.0 | 0.0 | 0.0 | 7.0 | 0.0 | 2.0 | 29.0 | 1.0 | 1.0 | 0.0 | 2.0 | 0.0 | 1.0 |
| 154 | 18.0 | 12.0 | 2.0 | 8.0 | 0.0 | 1.0 | 113.0 | 0.0 | 5.0 | 92.5 | 1.0 | 1.0 | 0.0 | 1.0 | 0.0 | 4.0 |
| 155 | 1.0 | 27.5 | 3.0 | 18.0 | 0.0 | 0.0 | 61.5 | 0.0 | 1.0 | 44.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 156 | 0.0 | 13.5 | 4.5 | 26.5 | 0.0 | 4.0 | 42.0 | 20.0 | 23.0 | 109.5 | 0.0 | 0.0 | 0.0 | 1.0 | 6.0 | 6.0 |
| 157 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 14.0 | 0.0 | 0.0 | 31.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 158 | 7.0 | 24.5 | 0.0 | 13.0 | 0.0 | 1.0 | 53.0 | 0.0 | 10.0 | 55.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 159 | 44.5 | 55.5 | 4.0 | 16.0 | 0.0 | 0.0 | 76.5 | 0.0 | 0.0 | 61.5 | 1.0 | 1.0 | 0.0 | 1.0 | 0.0 | 0.0 |
| 160 | 1.0 | 61.0 | 3.0 | 21.0 | 0.0 | 1.0 | 73.0 | 3.0 | 0.0 | 68.5 | 1.0 | 0.0 | 1.0 | 4.0 | 0.0 | 0.0 |
| 161 | 0.0 | 17.0 | 3.0 | 20.0 | 0.0 | 0.0 | 133.0 | 0.0 | 0.0 | 50.0 | 0.0 | 0.0 | 0.0 | 18.0 | 0.0 | 0.0 |
| 162 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 | 16.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 163 | 51.5 | 7.0 | 2.0 | 41.0 | 0.0 | 1.0 | 99.0 | 26.0 | 47.5 | 189.5 | 10.0 | 1.0 | 9.0 | 2.0 | 1.0 | 13.0 |
| 164 | 4.0 | 20.0 | 1.0 | 12.0 | 0.0 | 0.0 | 33.0 | 3.0 | 0.0 | 95.0 | 15.0 | 0.0 | 15.0 | 57.0 | 0.0 | 2.0 |
| 165 | 14.5 | 27.0 | 0.0 | 8.0 | 0.0 | 2.0 | 56.0 | 0.0 | 1.0 | 134.0 | 19.0 | 1.0 | 18.0 | 51.0 | 2.0 | 3.0 |

**6) 4 July 1992**

30 nests (numbers 166-195) were collected by LWP and KAK from site 12. The VI and MA sexuals were counted and frozen on 6th and 7th July, 1992. The rest of the categories (including EVI and EMA) were counted between 8th and 10th July, 1992, inclusive.

**Notes:**

1) The 60 FA in nest #184 were comprised of 4 dealate and 56 alate females. The 56 alates were frozen for weighing and the 4 dealates were dissected. Three of the four were found to be virgins and the fourth, probably the mother, mated with large ovaries. This explains why VI = 59 below, whereas Appendix 3 shows that only 56 were weighed.

2) Four female/worker intercastes were found in nest #188 but they are not included in any of the totals for that nest below.

| COL | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA | EVI | EMA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 166 | 24.5 | 32.0 | 3.0 | 2.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 | 62.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 167 | 6.0 | 61.0 | 1.0 | 4.0 | 0.0 | 2.0 | 104.5 | 0.0 | 0.0 | 107.0 | 10.0 | 1.0 | 9.0 | 2.0 | 0.0 | 0.0 |
| 168 | 0.0 | 3.0 | 3.0 | 14.0 | 0.0 | 1.0 | 28.0 | 0.0 | 0.0 | 56.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 169 | 5.0 | 57.5 | 0.0 | 0.0 | 0.0 | 0.0 | 17.0 | 0.0 | 0.0 | 62.5 | 1.0 | 0.0 | 1.0 | 4.0 | 0.0 | 0.0 |
| 170 | 19.0 | 53.0 | 2.0 | 6.0 | 0.0 | 0.0 | 120.5 | 0.0 | 0.0 | 75.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 1.0 |
| 171 | 0.0 | 1.0 | 0.0 | 2.0 | 0.0 | 0.0 | 53.0 | 0.0 | 0.0 | 89.5 | 6.0 | 0.0 | 6.0 | 0.0 | 0.0 | 0.0 |
| 172 | 25.5 | 49.5 | 12.5 | 26.0 | 0.0 | 1.0 | 47.0 | 0.0 | 0.0 | 84.5 | 1.0 | 1.0 | 0.0 | 5.0 | 0.0 | 1.0 |
| 173 | 8.0 | 24.0 | 1.0 | 2.0 | 0.0 | 1.0 | 10.0 | 0.0 | 8.0 | 42.0 | 0.0 | 0.0 | 0.0 | 30.0 | 0.0 | 3.0 |
| 174 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 33.0 | 0.0 | 0.0 | 47.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 175 | 13.5 | 78.0 | 0.0 | 0.0 | 0.0 | 0.0 | 66.5 | 0.0 | 0.0 | 190.0 | 5.0 | 1.0 | 4.0 | 0.0 | 1.0 | 0.0 |
| 176 | 1.0 | 36.5 | 0.0 | 14.0 | 0.0 | 0.0 | 66.0 | 0.0 | 0.0 | 124.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 177 | 0.0 | 8.0 | 0.0 | 3.0 | 0.0 | 0.0 | 47.0 | 0.0 | 0.0 | 86.0 | 0.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 |
| 178 | 30.5 | 48.5 | 0.0 | 6.0 | 0.0 | 0.0 | 63.0 | 0.0 | 0.0 | 89.0 | 1.0 | 1.0 | 0.0 | 6.0 | 0.0 | 0.0 |
| 179 | 18.5 | 60.0 | 0.0 | 2.0 | 0.0 | 0.0 | 42.0 | 0.0 | 0.0 | 158.5 | 1.0 | 1.0 | 0.0 | 2.0 | 0.0 | 0.0 |
| 180 | 7.0 | 38.0 | 0.0 | 4.0 | 0.0 | 0.0 | 55.0 | 0.0 | 0.0 | 221.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 181 | 10.0 | 33.5 | 0.0 | 4.0 | 0.0 | 0.0 | 38.0 | 0.0 | 0.0 | 81.0 | 10.0 | 1.0 | 9.0 | 0.0 | 0.0 | 0.0 |
| 182 | 1.0 | 18.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 19.0 | 0.0 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 |
| 183 | 0.0 | 4.0 | 0.0 | 0.0 | 0.0 | 0.0 | 13.0 | 0.0 | 0.0 | 46.0 | 0.0 | 0.0 | 0.0 | 28.0 | 0.0 | 0.0 |
| 184 | 17.0 | 89.0 | 0.0 | 13.0 | 0.0 | 3.0 | 140.0 | 2.0 | 0.0 | 191.0 | 60.0 | 1.0 | 59.0 | 11.0 | 6.0 | 1.0 |
| 185 | 0.0 | 6.0 | 0.0 | 3.0 | 0.0 | 2.0 | 82.5 | 0.0 | 0.0 | 153.0 | 4.0 | 0.0 | 4.0 | 1.0 | 0.0 | 0.0 |
| 186 | 23.0 | 54.0 | 0.0 | 0.0 | 0.0 | 0.0 | 91.0 | 0.0 | 0.0 | 276.0 | 34.0 | 1.0 | 33.0 | 2.0 | 0.0 | 0.0 |
| 187 | 25.0 | 68.5 | 0.0 | 2.0 | 0.0 | 0.0 | 60.0 | 0.0 | 0.0 | 247.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 188 | 8.5 | 34.5 | 1.0 | 2.0 | 0.0 | 0.0 | 31.0 | 0.0 | 0.0 | 113.5 | 2.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 189 | 0.0 | 5.0 | 0.0 | 7.0 | 0.0 | 1.0 | 62.0 | 0.0 | 0.0 | 74.5 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 |
| 190 | 0.0 | 3.0 | 0.0 | 19.0 | 0.0 | 3.0 | 129.0 | 0.0 | 0.0 | 83.5 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 |
| 191 | 17.0 | 67.5 | 1.0 | 12.0 | 0.0 | 2.0 | 96.5 | 0.0 | 3.0 | 171.5 | 15.0 | 1.0 | 14.0 | 8.0 | 0.0 | 0.0 |
| 192 | 10.0 | 30.0 | 0.0 | 2.0 | 0.0 | 0.0 | 23.0 | 0.0 | 0.0 | 79.5 | 9.0 | * | * | 0.0 | 0.0 | 0.0 |
| 193 | 40.0 | 63.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 58.5 | 1.0 | 0.0 | 1.0 | 15.0 | 2.0 | 0.0 |
| 194 | 5.0 | 26.5 | 5.0 | 26.0 | 0.0 | 1.0 | 126.5 | 0.0 | 0.0 | 130.5 | 1.0 | 1.0 | 0.0 | 3.0 | 0.0 | 0.0 |
| 195 | 43.5 | 32.0 | 1.0 | 10.5 | 0.0 | 2.0 | 139.5 | 0.0 | 0.0 | 110.5 | 20.0 | 1.0 | 19.0 | 13.0 | 6.0 | 0.0 |

**7) <u>20 July 1992</u>**

30 nests (numbers 196-225) were collected by LWP and KAK from sites 13 to 16 inclusive. The VI and MA sexuals were counted and frozen on 21st July, 1992. The rest of the categories (including EVI and EMA) were counted between 22nd and 24th July, 1992, inclusive. No EMA at all were found.

One female/worker intercaste individual was found in nest #214, but it is not included in any of the totals for that nest below.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA | EVI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 196 | 1 | 27.5 | 26.0 | 4.0 | 7.0 | 0.0 | 0.0 | 50.0 | 0.0 | 0.0 | 72.0 | 2.0 | 1.0 | 1.0 | 15.0 | 0.0 |
| 197 | 1 | 13.5 | 68.5 | 1.0 | 0.0 | 0.0 | 1.0 | 37.0 | 0.0 | 0.0 | 117.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 198 | 0 | 3.0 | 12.0 | 0.0 | 0.0 | 0.0 | 0.0 | 94.0 | 0.0 | 0.0 | 152.0 | 2.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 199 | 0 | 4.0 | 57.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 142.0 | 1.0 | 1.0 | 0.0 | 7.0 | 0.0 |
| 200 | 0 | 3.0 | 26.5 | 0.0 | 3.0 | 0.0 | 0.0 | 19.0 | 0.0 | 0.0 | 76.5 | 2.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 201 | 0 | 22.5 | 26.0 | 1.0 | 6.0 | 0.0 | 0.0 | 7.0 | 0.0 | 0.0 | 66.0 | 1.0 | 1.0 | 0.0 | 1.0 | 0.0 |
| 202 | 0 | 18.0 | 101.5 | 0.0 | 1.0 | 0.0 | 0.0 | 40.0 | 0.0 | 0.0 | 315.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 203 | 1 | 19.0 | 29.0 | 0.0 | 5.0 | 0.0 | 0.0 | 61.0 | 0.0 | 0.0 | 198.5 | 4.0 | 1.0 | 3.0 | 0.0 | 0.0 |
| 204 | 0 | 20.5 | 85.5 | 1.0 | 2.0 | 0.0 | 0.0 | 136.5 | 0.0 | 0.0 | 187.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 205 | 0 | 0.0 | 1.0 | 5.0 | 1.0 | 0.0 | 0.0 | 27.0 | 0.0 | 0.0 | 92.5 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 |
| 206 | 1 | 12.5 | 19.0 | 0.0 | 0.0 | 0.0 | 0.0 | 6.0 | 0.0 | 0.0 | 177.0 | 2.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 207 | 0 | 17.5 | 41.0 | 0.0 | 2.0 | 0.0 | 0.0 | 47.5 | 0.0 | 0.0 | 209.0 | 6.0 | 1.0 | 5.0 | 1.0 | 0.0 |
| 208 | 1 | 29.0 | 18.0 | 0.0 | 2.0 | 0.0 | 0.0 | 14.0 | 0.0 | 0.0 | 74.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 209 | 1 | 1.0 | 7.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 19.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 210 | 1 | 57.0 | 61.0 | 1.0 | 18.5 | 0.0 | 7.5 | 165.5 | 6.0 | 0.0 | 248.5 | 10.0 | 1.0 | 9.0 | 2.0 | 18.0 |
| 211 | 0 | 53.0 | 77.0 | 0.0 | 4.0 | 0.0 | 0.0 | 47.5 | 0.0 | 0.0 | 241.0 | 5.0 | 1.0 | 4.0 | 1.0 | 0.0 |
| 212 | 1 | 43.5 | 48.5 | 1.0 | 5.0 | 0.0 | 0.0 | 25.0 | 0.0 | 0.0 | 114.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 213 | 1 | 19.0 | 40.0 | 0.0 | 6.0 | 0.0 | 1.0 | 28.0 | 0.0 | 0.0 | 152.5 | 1.0 | 1.0 | 0.0 | 10.0 | 0.0 |
| 214 | 1 | 42.5 | 59.0 | 0.0 | 1.0 | 0.0 | 0.0 | 18.0 | 0.0 | 0.0 | 172.5 | 26.0 | 1.0 | 25.0 | 0.0 | 0.0 |
| 215 | 1 | 1.0 | 13.0 | 0.0 | 0.0 | 0.0 | 0.0 | 39.0 | 0.0 | 1.0 | 87.5 | 0.0 | 0.0 | 0.0 | 69.0 | 0.0 |
| 216 | 1 | 46.5 | 99.0 | 0.0 | 7.0 | 0.0 | 0.0 | 113.0 | 0.0 | 0.0 | 200.0 | 33.0 | 1.0 | 32.0 | 34.0 | 0.0 |
| 217 | 0 | 39.0 | 42.5 | 1.0 | 3.0 | 0.0 | 0.0 | 16.0 | 0.0 | 0.0 | 211.0 | 16.0 | 1.0 | 15.0 | 20.0 | 2.0 |
| 218 | 0 | 48.5 | 65.0 | 1.0 | 2.0 | 0.0 | 1.0 | 14.0 | 0.0 | 0.0 | 206.0 | 1.0 | 1.0 | 0.0 | 1.0 | 0.0 |
| 219 | 0 | 50.5 | 39.0 | 4.0 | 3.0 | 0.0 | 0.0 | 38.0 | 0.0 | 0.0 | 63.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 220 | 0 | 21.0 | 62.0 | 0.0 | 0.0 | 0.0 | 0.0 | 29.0 | 0.0 | 0.0 | 308.0 | 15.0 | 1.0 | 14.0 | 1.0 | 0.0 |
| 221 | 0 | 18.0 | 64.5 | 0.0 | 0.0 | 0.0 | 3.0 | 94.5 | 0.0 | 0.0 | 176.5 | 10.0 | 1.0 | 9.0 | 12.0 | 0.0 |
| 222 | 0 | 11.0 | 40.5 | 0.0 | 3.0 | 0.0 | 0.0 | 23.0 | 0.0 | 0.0 | 60.0 | 1.0 | 1.0 | 0.0 | 14.0 | 0.0 |
| 223 | 0 | 67.5 | 36.0 | 0.0 | 6.0 | 0.0 | 0.0 | 62.0 | 0.0 | 0.0 | 223.0 | 1.0 | 1.0 | 0.0 | 16.0 | 0.0 |
| 224 | 1 | 13.0 | 34.0 | 2.0 | 0.0 | 0.0 | 0.0 | 32.0 | 0.0 | 0.0 | 111.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 225 | 1 | 12.0 | 14.0 | 0.0 | 2.0 | 0.0 | 0.0 | 7.0 | 0.0 | 0.0 | 25.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

**8) 8 August 1992**

30 nests (numbers 226-255) were collected by LWP and KAK from site 17. The VI and MA sexuals were counted and frozen on 10th August, 1992. The rest of the categories were counted between 10th and 12th August, 1992, inclusive.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 226 | 1 | 57.5 | 63.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 | 231.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 227 | 0 | 45.5 | 25.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 60.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 228 | 0 | 73.5 | 64.5 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 231.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 229 | 1 | 65.5 | 36.5 | 0.0 | 3.0 | 0.0 | 0.0 | 7.0 | 0.0 | 0.0 | 152.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 230 | 1 | 31.5 | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 112.5 | 6.0 | 1.0 | 5.0 | 0.0 |
| 231 | 1 | 27.5 | 28.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 | 185.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 232 | 0 | 72.5 | 82.0 | 0.0 | 1.0 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 235.5 | 2.0 | 1.0 | 1.0 | 0.0 |
| 233 | 0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 13.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 234 | 1 | 69.5 | 37.5 | 1.0 | 0.0 | 0.0 | 0.0 | 34.0 | 0.0 | 0.0 | 80.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 235 | 0 | 0.0 | 3.0 | 0.0 | 1.0 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 59.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 236 | 1 | 31.0 | 39.5 | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | 0.0 | 1.0 | 178.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 237 | 0 | 136.5 | 102.5 | 1.0 | 0.0 | 0.0 | 0.0 | 4.0 | 0.0 | 0.0 | 99.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 238 | 1 | 107.5 | 121.5 | 0.0 | 0.0 | 0.0 | 0.0 | 14.0 | 0.0 | 0.0 | 360.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 239 | 1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 12.0 | 0.0 | 0.0 | 46.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 240 | 1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 6.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 241 | 0 | 63.5 | 75.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 0.0 | 0.0 | 198.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 242 | 0 | 58.0 | 70.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 144.5 | 2.0 | 1.0 | 1.0 | 0.0 |
| 243 | 1 | 24.5 | 51.5 | 0.0 | 1.0 | 0.0 | 0.0 | 37.5 | 0.0 | 0.0 | 392.0 | 1.0 | 0.0 | 1.0 | 0.0 |
| 244 | 0 | 32.5 | 16.0 | 0.0 | 3.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 54.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 245 | 0 | 50.0 | 22.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 216.0 | 2.0 | 1.0 | 1.0 | 0.0 |
| 246 | 0 | 59.5 | 52.0 | 0.0 | 1.0 | 0.0 | 0.0 | 21.0 | 0.0 | 0.0 | 120.5 | 2.0 | 1.0 | 1.0 | 0.0 |
| 247 | 1 | 18.5 | 28.5 | 0.0 | 2.0 | 0.0 | 0.0 | 4.0 | 0.0 | 0.0 | 204.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 248 | 1 | 0.0 | 9.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 | 31.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 249 | 0 | 0.0 | 4.0 | 0.0 | 0.0 | 0.0 | 0.0 | 7.0 | 0.0 | 0.0 | 71.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 250 | 0 | 94.5 | 79.0 | 0.0 | 0.0 | 0.0 | 0.0 | 59.0 | 0.0 | 0.0 | 188.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 251 | 1 | 103.0 | 28.5 | 0.0 | 0.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 167.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 252 | 1 | 62.5 | 118.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 125.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 253 | 0 | 3.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 13.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 254 | 0 | 47.5 | 59.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 0.0 | 0.0 | 197.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 255 | 1 | 51.5 | 23.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 182.0 | 1.0 | 1.0 | 0.0 | 0.0 |

**9) <u>29 August 1992</u>**

33 nests (numbers 256-288) were collected by LWP and KAK from site 18. The VI and MA sexuals were counted and frozen on 31st August, 1992. The rest of the categories (including EVI and EMA) were counted between 31st August and 4th September, 1992, inclusive. No EVI were found.

Four intercaste female/worker individuals were found: two in nest #261, and one in nest #269. The fourth intercaste was not found until a day after nests 259 and 263 had been fused together in an experiment begun on 4.9.92. This individual could have therefore come from either of the nests. None of these four intercastes have been included in the totals below.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA | EMA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 256 | 0 | 56.5 | 78.5 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 227.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 257 | 1 | 90.0 | 54.5 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 371.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 258 | 0 | 4.0 | 25.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 0.0 | 0.0 | 18.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 259 | 1 | 17.5 | 18.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 72.0 | 2.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 260 | 1 | 38.5 | 93.5 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 187.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 261 | 1 | 64.0 | 95.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 206.0 | 4.0 | 1.0 | 3.0 | 0.0 | 0.0 |
| 262 | 0 | 31.5 | 68.5 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 202.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 263 | 0 | 25.0 | 50.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 54.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 |
| 264 | 0 | 60.5 | 93.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 1.0 | 0.0 | 407.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 265 | 0 | 60.0 | 76.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 145.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 266 | 0 | 5.0 | 24.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 28.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 267 | 1 | 45.5 | 57.0 | 0.0 | 0.0 | 0.0 | 0.0 | 7.0 | 0.0 | 0.0 | 255.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 268 | 0 | 9.5 | 74.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 77.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 269 | 0 | 41.5 | 122.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 240.0 | 2.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 270 | 1 | 38.5 | 136.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 362.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 271 | 1 | 28.0 | 89.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 156.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 272 | 1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 7.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 273 | 0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 28.5 | 2.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 274 | 1 | 14.0 | 145.5 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 | 177.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 275 | 1 | 0.0 | 13.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 68.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 276 | 0 | 11.5 | 21.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 125.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 277 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 48.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 278 | 1 | 50.0 | 100.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 220.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 279 | 1 | 27.0 | 128.5 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 179.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 280 | 1 | 65.0 | 99.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 221.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 281 | 0 | 70.0 | 63.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 333.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 282 | 0 | 364.5 | 93.0 | 0.0 | 0.0 | 2.0 | 0.0 | 1.0 | 0.0 | 0.0 | 168.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 283 | 1 | 49.0 | 129.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 213.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 284 | 1 | 49.0 | 105.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 192.0 | 3.0 | 2.0 | 1.0 | 0.0 | 0.0 |
| 285 | 0 | 38.5 | 121.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 0.0 | 0.0 | 219.0 | 5.0 | 1.0 | 4.0 | 0.0 | 0.0 |
| 286 | 1 | 7.0 | 13.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 30.5 | 1.0 | 0.0 | 1.0 | 0.0 | 0.0 |
| 287 | 1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 288 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 |

**10) 17 September 1992**

30 nests (numbers 289-318) were collected by LWP and KAK from site 19. The VI and MA sexuals were counted and frozen on 18th September, 1992. The rest of the categories were counted between 21st and 23rd September, 1992, inclusive.

A single gynandromorph was found in nest #317. It has not been included in any of the totals for that nest below.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 289 | 0 | 24.0 | 86.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 186.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 290 | 1 | 34.0 | 200.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 164.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 291 | 1 | 39.5 | 134.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 203.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 292 | 1 | 28.0 | 70.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 126.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 293 | 0 | 53.0 | 168.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 345.0 | 3.0 | 1.0 | 2.0 | 0.0 |
| 294 | 0 | 59.0 | 108.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 164.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 295 | 0 | 5.0 | 125.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 225.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 296 | 0 | 40.5 | 97.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 211.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 297 | 1 | 37.5 | 123.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 232.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 298 | 1 | 19.0 | 108.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 236.0 | 3.0 | 1.0 | 2.0 | 0.0 |
| 299 | 0 | 19.0 | 198.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 236.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 300 | 1 | 50.0 | 156.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 213.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 301 | 0 | 16.0 | 56.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 155.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 302 | 1 | 37.5 | 113.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 250.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 303 | 0 | 25.5 | 102.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 108.0 | 2.0 | 1.0 | 1.0 | 0.0 |
| 304 | 0 | 14.5 | 40.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 91.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 305 | 0 | 4.0 | 174.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 214.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 306 | 1 | 21.0 | 144.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 237.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 307 | 0 | 95.5 | 80.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 120.0 | 17.0 | 0.0 | 17.0 | 0.0 |
| 308 | 1 | 11.0 | 244.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 205.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 309 | 0 | 18.0 | 149.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 262.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 310 | 1 | 14.5 | 151.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 220.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 311 | 0 | 27.0 | 62.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 159.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 312 | 1 | 14.0 | 77.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 232.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 313 | 1 | 77.0 | 110.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 180.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 314 | 0 | 48.5 | 253.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 322.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 315 | 1 | 9.5 | 77.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 176.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 316 | 1 | 9.0 | 72.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 161.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 317 | 0 | 42.5 | 151.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 338.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 318 | 0 | 21.5 | 104.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 190.5 | 3.0 | 1.0 | 2.0 | 0.0 |

**11) 22 October 1992**

30 nests (numbers 319-348) were collected by LWP and KAK from site 20. The nest contents were counted on 26th and 27th October, 1992.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 319 | 1 | 0.0 | 134.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 156.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 320 | 0 | 0.0 | 22.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 37.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 321 | 0 | 2.0 | 223.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 139.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 322 | 0 | 2.0 | 128.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 119.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 323 | 1 | 6.5 | 174.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 182.0 | 2.0 | * | * | 0.0 |
| 324 | 1 | 21.0 | 124.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 210.5 | 2.0 | * | * | 0.0 |
| 325 | 0 | 8.5 | 171.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 192.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 326 | 0 | 6.0 | 187.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 235.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 327 | 0 | 8.0 | 156.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 189.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 328 | 1 | 7.5 | 125.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 277.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 329 | 0 | 20.0 | 135.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 185.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 330 | 1 | 0.0 | 83.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 129.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 331 | 1 | 7.5 | 142.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 225.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 332 | 1 | 0.0 | 11.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 14.0 | 3.0 | 0.0 | 3.0 | 0.0 |
| 333 | 1 | 0.0 | 235.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 346.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 334 | 0 | 6.5 | 117.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 195.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 335 | 1 | 9.5 | 119.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 100.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 336 | 1 | 3.0 | 73.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 76.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 337 | 0 | 26.0 | 60.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 217.0 | 3.0 | * | * | 0.0 |
| 338 | 1 | 0.0 | 269.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 370.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 339 | 1 | 3.0 | 154.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 213.5 | 2.0 | * | * | 0.0 |
| 340 | 1 | 7.0 | 162.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 176.5 | 2.0 | * | * | 0.0 |
| 341 | 0 | 17.0 | 119.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 289.0 | 2.0 | * | * | 0.0 |
| 342 | 1 | 2.0 | 169.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 139.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 343 | 0 | 4.0 | 55.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 96.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 344 | 0 | 2.0 | 255.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 317.0 | 2.0 | * | * | 0.0 |
| 345 | 0 | 0.0 | 122.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 108.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 346 | 0 | 5.5 | 142.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 243.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 347 | 1 | 2.5 | 107.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 230.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 348 | 0 | 15.5 | 217.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 338.0 | 1.0 | 1.0 | 0.0 | 0.0 |

**12) <u>21 November 1992</u>**

30 nests (numbers 349-378) were collected by LWP and KAK from site 21 (note that nest #349 was collected by GBB). The nest contents were counted on 24th and 25th November, 1992.

One intercaste female/worker individual was found in nest #359, but it has not been included in any of the totals for that nest below.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 349 | 2 | 0.0 | 21.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 55.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 350 | 0 | 4.0 | 106.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 140.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 351 | 1 | 18.5 | 153.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 213.0 | 2.0 | 1.0 | 1.0 | 0.0 |
| 352 | 1 | 31.0 | 143.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 179.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 353 | 0 | 7.0 | 131.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 271.5 | 1.0 | 0.0 | 1.0 | 0.0 |
| 354 | 1 | 2.0 | 126.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 154.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 355 | 1 | 7.0 | 161.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 274.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 356 | 0 | 5.0 | 134.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 182.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 357 | 0 | 3.0 | 90.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 164.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 358 | 1 | 11.5 | 19.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 45.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 359 | 0 | 4.0 | 122.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 201.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 360 | 1 | 11.0 | 269.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 325.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 361 | 1 | 0.0 | 29.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 22.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 362 | 0 | 4.5 | 15.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 24.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 363 | 0 | 17.5 | 126.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 168.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 364 | 1 | 29.5 | 152.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 221.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 365 | 0 | 15.0 | 214.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 367.5 | 2.0 | * | * | 0.0 |
| 366 | 0 | 25.0 | 183.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 241.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 367 | 1 | 1.0 | 44.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 46.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 368 | 1 | 4.0 | 125.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 184.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 369 | 0 | 20.5 | 158.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 213.5 | 3.0 | 1.0 | 2.0 | 0.0 |
| 370 | 0 | 7.5 | 165.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 175.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 371 | 1 | 8.0 | 88.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 61.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 372 | 0 | 3.0 | 98.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 123.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 373 | 0 | 5.0 | 66.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 114.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 374 | 0 | 8.5 | 153.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 262.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 375 | 1 | 10.0 | 162.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 229.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 376 | 0 | 5.0 | 191.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 372.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 377 | 1 | 11.0 | 130.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 204.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 378 | 1 | 9.5 | 207.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 314.0 | 1.0 | 1.0 | 0.0 | 0.0 |

**13) 15 December 1992**

30 nests (numbers 379-408) were collected by LWP and GMO (not KAK) from site 22. The nest contents were counted between 16th and 18th December, 1992, inclusive.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 379 | 1 | 40.0 | 192.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 268.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 380 | 1 | 3.0 | 52.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 172.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 381 | 3 | 10.5 | 123.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 256.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 382 | 3 | 3.0 | 127.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 193.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 383 | 3 | 10.0 | 90.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 162.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 384 | 1 | 9.5 | 128.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 170.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 385 | 3 | 3.0 | 67.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 128.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 386 | 3 | 1.0 | 140.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 241.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 387 | 1 | 2.5 | 136.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 201.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 388 | 1 | 19.0 | 143.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 309.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 389 | 3 | 7.0 | 165.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 246.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 390 | 3 | 3.0 | 95.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 61.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 391 | 1 | 21.5 | 152.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 227.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 392 | 1 | 4.5 | 114.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 168.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 393 | 1 | 4.0 | 59.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 128.5 | 4.0 | 1.0 | 3.0 | 0.0 |
| 394 | 3 | 11.5 | 157.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 182.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 395 | 1 | 16.5 | 169.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 245.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 396 | 1 | 6.5 | 133.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 199.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 397 | 1 | 14.5 | 127.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 263.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 398 | 3 | 5.0 | 130.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 115.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 399 | 1 | 10.5 | 106.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 195.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 400 | 1 | 4.0 | 108.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 185.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 401 | 1 | 10.5 | 161.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 240.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 402 | 1 | 13.5 | 102.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 163.0 | 2.0 | 1.0 | 1.0 | 0.0 |
| 403 | 3 | 19.5 | 145.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 251.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 404 | 3 | 9.0 | 260.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 367.5 | 4.0 | 2.0 | 2.0 | 0.0 |
| 405 | 3 | 1.0 | 47.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 68.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 406 | 1 | 9.5 | 207.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 229.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 407 | 1 | 1.0 | 57.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 126.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 408 | 3 | 1.0 | 28.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 196.0 | 0.0 | 0.0 | 0.0 | 0.0 |

**14) 17 January 1993**

30 nests (numbers 409-438) were collected by LWP and KAK from site 23. The nest contents were counted on 19th and 20th January, 1993.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 409 | 0 | 15.5 | 119.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 180.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 410 | 0 | 4.0 | 134.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 169.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 411 | 1 | 2.0 | 49.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 83.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 412 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 1.0 | 0.0 | 1.0 | 0.0 |
| 413 | 1 | 7.0 | 192.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 215.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 414 | 0 | 0.0 | 22.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 61.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 415 | 0 | 5.5 | 182.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 208.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 416 | 0 | 4.0 | 195.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 221.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 417 | 1 | 1.0 | 233.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 232.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 418 | 1 | 8.0 | 92.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 106.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 419 | 1 | 1.0 | 192.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 220.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 420 | 1 | 3.0 | 97.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 220.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 421 | 0 | 4.0 | 179.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 176.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 422 | 1 | 17.5 | 191.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 392.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 423 | 1 | 4.0 | 58.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 148.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 424 | 0 | 2.0 | 90.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 44.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 425 | 1 | 0.0 | 15.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 40.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 426 | 0 | 7.0 | 166.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 269.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 427 | 0 | 12.0 | 112.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 151.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 428 | 0 | 16.0 | 200.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 264.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 429 | 1 | 0.0 | 253.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 295.5 | 3.0 | 1.0 | 2.0 | 0.0 |
| 430 | 1 | 11.5 | 64.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 111.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 431 | 0 | 8.0 | 151.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 242.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 432 | 0 | 2.0 | 13.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 59.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 433 | 1 | 13.0 | 174.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 414.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 434 | 0 | 17.0 | 250.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 303.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 435 | 1 | 3.0 | 102.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 171.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 436 | 1 | 13.0 | 243.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 298.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 437 | 0 | 5.0 | 83.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 108.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 438 | 0 | 6.0 | 169.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 315.0 | 1.0 | 1.0 | 0.0 | 0.0 |

**15) <u>20 February 1993</u>**

30 nests (numbers 439-469) were collected by LWP and KAK from site 24. The nest contents were counted on 23rd and 24th February, 1993.

Nest numbers 456 and 461 were found only 10cm apart in the same rock. It was thought that they belonged to the same colony and therefore the contents of nest #456 (which were only 2 ML and 17 WA) were added to nest #461. The workers of #456 were not attacked and the two larvae were taken inside the nest of #461 whereupon they were surrounded and bitten (but not eaten?) by many workers. The data for nest #456 are therefore entered as missing values below.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 439 | 0 | 7.0 | 148.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 117.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 440 | 1 | 7.5 | 150.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 275.0 | 2.0 | 1.0 | 1.0 | 0.0 |
| 441 | 0 | 4.0 | 141.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 251.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 442 | 0 | 2.0 | 62.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 104.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 443 | 1 | 12.0 | 155.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 250.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 444 | 0 | 4.0 | 154.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 275.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 445 | 1 | 17.5 | 76.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 133.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 446 | 1 | 23.0 | 118.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 155.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 447 | 1 | 8.5 | 142.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 214.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 448 | 1 | 3.0 | 74.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 165.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 449 | 0 | 6.0 | 149.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 197.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 450 | 0 | 2.0 | 167.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 236.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 451 | 0 | 1.0 | 82.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 166.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 452 | 0 | 6.0 | 144.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 109.5 | 2.0 | 2.0 | 0.0 | 0.0 |
| 453 | 0 | 2.0 | 98.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 81.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 454 | 1 | 0.0 | 120.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 188.0 | 2.0 | 1.0 | 1.0 | 0.0 |
| 455 | 1 | 1.0 | 155.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 217.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 456 | 1 | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| 457 | 0 | 0.0 | 64.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 127.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 458 | 0 | 5.0 | 167.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 251.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 459 | 1 | 11.5 | 261.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 335.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 460 | 1 | 4.0 | 12.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 35.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 461 | 1 | 11.0 | 215.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 285.5 | 2.0 | 2.0 | 0.0 | 0.0 |
| 462 | 0 | 6.0 | 203.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 277.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 463 | 1 | 6.5 | 95.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 152.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 464 | 1 | 23.5 | 174.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 348.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 465 | 0 | 7.0 | 120.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 270.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 466 | 1 | 0.0 | 54.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 117.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 467 | 0 | 8.0 | 98.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 170.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 468 | 1 | 6.5 | 238.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 306.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 469 | 0 | 0.0 | 102.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 96.5 | 1.0 | 1.0 | 0.0 | 0.0 |

**16) 27 March 1993**

30 nests (numbers 470-499) were collected by LWP and KAK from site 25. The nest contents were counted between 30th March and 2nd April, 1993, inclusive.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 470 | 0 | 3.0 | 119.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 255.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 471 | 1 | 1.0 | 105.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 73.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 472 | 1 | 3.0 | 31.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 65.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 473 | 0 | 2.0 | 157.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 239.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 474 | 1 | 0.0 | 112.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 211.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 475 | 0 | 6.0 | 141.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 291.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 476 | 1 | 15.0 | 109.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 180.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 477 | 0 | 6.5 | 40.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 148.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 478 | 0 | 10.5 | 98.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 121.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 479 | 1 | 0.0 | 64.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 60.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 480 | 0 | 6.0 | 102.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 171.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 481 | 0 | 17.5 | 129.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 209.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 482 | 1 | 8.0 | 225.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 321.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 483 | 1 | 0.0 | 122.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 109.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 484 | 0 | 11.0 | 38.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 59.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 485 | 1 | 3.0 | 177.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 195.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 486 | 1 | 4.5 | 300.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 380.5 | 2.0 | 2.0 | 0.0 | 0.0 |
| 487 | 1 | 1.0 | 210.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 290.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 488 | 0 | 20.0 | 72.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 166.5 | 2.0 | 2.0 | 0.0 | 0.0 |
| 489 | 0 | 10.0 | 68.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 165.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 490 | 1 | 12.5 | 203.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 284.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 491 | 0 | 5.0 | 169.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 225.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 492 | 1 | 8.5 | 212.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 325.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 493 | 0 | 12.0 | 218.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 248.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 494 | 0 | 3.0 | 155.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 230.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 495 | 1 | 0.0 | 77.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 61.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 496 | 0 | 3.0 | 123.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 285.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 497 | 1 | 2.0 | 127.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 178.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 498 | 1 | 13.0 | 216.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 257.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 499 | 0 | 2.0 | 85.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 99.0 | 1.0 | 1.0 | 0.0 | 0.0 |

**17) 1 May 1993**

30 nests (numbers 500-529) were collected by LWP and KAK from site 26. The nest contents were counted between 4th and 6th May, 1993, inclusive.

| COL | SA | EM | ML | LL | WPP | FPP | MPP | WP | FP | MP | WA | FA | MO | VI | MA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 500 | 1 | 2.0 | 112.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 112.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 501 | 1 | 7.5 | 147.0 | 25.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 148.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 502 | 0 | 0.0 | 47.5 | 4.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 53.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 503 | 1 | 2.0 | 230.5 | 27.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 162.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 504 | 0 | 1.0 | 90.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 102.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 505 | 0 | 3.0 | 130.0 | 31.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 125.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 506 | 0 | 9.0 | 55.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 72.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 507 | 0 | 31.5 | 139.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 92.5 | 1.0 | * | * | 0.0 |
| 508 | 1 | 4.5 | 123.5 | 19.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 124.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 509 | 0 | 0.0 | 14.0 | 7.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 43.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 510 | 0 | 2.0 | 103.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 82.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 511 | 0 | 4.0 | 209.0 | 20.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 294.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 512 | 1 | 30.5 | 38.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 44.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 513 | 1 | 0.0 | 90.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 140.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 514 | 0 | 3.0 | 58.5 | 34.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 86.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 515 | 0 | 2.0 | 95.5 | 3.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 92.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 516 | 1 | 8.0 | 57.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 57.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 517 | 1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 9.0 | 2.0 | 0.0 | 2.0 | 0.0 |
| 518 | 1 | 0.0 | 87.5 | 9.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 199.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 519 | 0 | 15.0 | 40.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 57.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 520 | 0 | 22.5 | 158.5 | 5.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 219.5 | 2.0 | 2.0 | 0.0 | 0.0 |
| 521 | 0 | 0.0 | 156.0 | 16.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 119.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 522 | 1 | 0.0 | 22.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 45.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 523 | 0 | 6.5 | 95.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 127.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 524 | 1 | 0.0 | 129.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 221.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 525 | 1 | 22.0 | 129.5 | 9.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 167.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 526 | 1 | 5.0 | 223.5 | 26.0 | 6.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 178.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 527 | 1 | 9.5 | 54.0 | 4.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 42.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 528 | 0 | 15.5 | 134.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 186.5 | 1.0 | 1.0 | 0.0 | 0.0 |
| 529 | 1 | 2.0 | 334.0 | 33.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 332.5 | 2.0 | 2.0 | 0.0 | 0.0 |

## Appendix 3

## Sexual dry weight data for the *Leptothorax tuberointerruptus* study

This appendix lists the dry weights of the male and female adult sexuals taken from the nests of *Leptothorax tuberointerruptus*.

The sexuals to be weighed were transferred from their nests to petri dishes and placed in a -40°C freezer to kill and store the sexuals prior to drying. When it came to drying the sexuals, each one was put in a uniquely numbered 0.5ml capped Eppendorf tube (Sarstedt). The tubes were mixed up and placed in random order, with their lids open, in every other hole of a series of microtitre plates. The microtitre plates were then placed in a drying oven set to 50°C constant temperature. A higher temperature would have caused lipids to sublime (N.R. Franks, pers. comm.). A sample of ten sexuals (several of each sex, and from different parts of the oven) was weighed every few days. All the sexuals were assumed to have dried once the average change in weight of the ten individuals between two successive weighings was only about 2$\mu$g. This usually took a week or so to occur.

The tubes were closed as soon as they were removed from the oven and only opened immediately prior to the removal of each individual for weighing. This reduced the error due to moisture gain (and hence weight gain) from the relatively humid atmosphere. The tubes were left to cool by the

balance for at least an hour to prevent temperature differences from affecting the weight measurements. The sexuals were weighed in random order using an automatically calibrated Mettler UM2 six-figure digital balance. The condition of each sexual (see below); weighing order (so that the data could be checked later to see if the sexuals were weighed in random order); and its weight to the nearest microgram were recorded. The balance was rezeroed between each weighing.

The condition of each sexual was later coded numerically by answering yes or no to each of the following three questions and then consulting a table similar to Table A3.1 below.

Q1: Are all parts of the body present (including the wings)?

Q2: Are all the parts that are present still connected together?

Q3: Is the sexual apparently mature?

A sexual was considered immature if any of its wings were still encased in their pupal cuticle; or, if the wings had lost their pupal sheaths following eclosion, then they had not yet fully expanded and were still somewhat milky opaque and crumpled in appearance. A sexual was considered mature if it was fully dealate, or if all of the wings that it still had were fully expanded and transparent. Although this operational definition of maturity depended to a large extent on the presence of wings, the occurrence of immature individuals that had lost all four of their unexpanded wings, and which would have therefore been mistakenly

classified as mature, was considered to be unlikely. This last statement was supported by the preponderance of condition code 1 sexuals A3.1 among the final data.

**Table A3.1 Table showing how a single numerical code could be assigned to each sexual according to its condition (Y = yes; N = no). Questions Q1 to Q3 are explained in the text.**

| Answers to questions | | | Code number |
|---|---|---|---|
| Q1 | Q2 | Q3 | |
| Y | Y | Y | 1 |
| Y | Y | N | 2 |
| Y | N | Y | 3 |
| Y | N | N | 4 |
| N | Y | Y | 5 |
| N | Y | N | 6 |
| N | N | Y | 7 |
| N | N | N | 8 |

Q1 is obviously important because an absence of parts will result in a lower weight. Q2 is important because a broken body may lose more weight than an unbroken one due to the direct exposure of the viscera to the dry air in the former. Q3 is important because it allows the weights of young and old sexuals of both sexes to be compared; there are almost certainly sex-specific changes in weight of a sexual between the times of eclosion and mating (eg., see Peakin, 1972, and Boomsma and Isaaks, 1985).

Some sexuals were removed from their colonies for drying and weighing before the rest of the colony categories were counted. These correspond to the VI and MA categories in Appendix 2 and are here called 'early' sexuals. However, on several occasions, some extra sexuals had emerged by the time the rest of the colony categories came to be counted.

These were the EVI and EMA categories listed in Appendix 2. Eventually, at various times after their collection, the colonies were all anaesthetised with $CO_2$ gas and then frozen to -70°C. Any sexuals still present then were separated and then dried and weighed in the same way as the early sexuals. To distinguish them from the early sexuals these sexuals were called 'late' sexuals. Thus the late sexuals may have contained some of the individuals already counted among the EVI and EMA categories, but many would have eclosed as adults after the colony categories had been counted.

Unlike, the early sexuals, the late sexuals were present in the artificial laboratory conditions for some time and were kept with the workers in petri dishes, which had a constant supply of tap water, honey solution and *Drosophila* larvae for food. However, the data for the late sexuals are included here because, by comparing them with the data for the early sexuals collected on several dates, some assessment of the impact of laboratory conditions (and potentially unrestricted access to unlimited food), and also of the weight changes following eclosion, could in principle be made.

Table A3.2 below shows the numbers of early and late sexuals, and the dates on which they were frozen. A sensible strategy for preliminary analysis of the dry weight data would be to confine attention to the code 1 early sexuals taken from the nests found on 20th June and 4th and 20th July, 1992.

**Table A3.2 Table showing the number of early and late sexuals collected, the number of colonies from which they were taken, and the dates on which they were taken and frozen. On the dates where only one sexual was found, the number of the parent nest and the sex of the sexual are given in parentheses (M = male; F = female).**

| Date nests were collected (1992) | Date(s) early sexuals were frozen (1992) | Dates over which the rest of the categories were counted (1992) | Number of nests from which early sexuals were taken | Number of early sexuals | Date(s) late sexuals were frozen (1992) | Number of nests from which late sexuals were taken | Number of late sexuals | Total number of sexuals frozen (early plus late) |
|---|---|---|---|---|---|---|---|---|
| 20 June | 22-23 June | 24-26 June | 23 | 535 | 14-15 July | 15 | 436 | 971 |
| 4 July | 6-7 July | 8-10 July | 24 | 314 | 13-14 July | 6 | 17 | 331 |
| 20 July | 21 July | 22-24 July | 21 | 326 | 27 July | 2 | 27 | 353 |
| 8 August | 10 August | 10-12 August | 1 (#230) | 1 (F) | - | 0 | 0 | 1 |
| 29 August | 31 August | 31 Aug.-4 Sept. | 1 (#285) | 1 (F) | 5 Sept. | 1 (#263) | 1 (M) | 2 |
| 17 Sept. | 18 Sept. | 21-23 Sept. | 1 (#293) | 1 (F) | - | 0 | 0 | 1 |
| Totals: | - | - | 71 | 1178 | - | 24 | 481 | 1659 |

The sexuals were dried and weighed in two batches. Batch #1 comprised the 971 sexuals taken from the nests collected on 20th June, 1992. All of the remaining 688 sexuals were weighed in batch #2. The data are presented in columns with the following headings:

TUB = number of TUBe containing the sexual; ie., a number unique to the sexual in the batch it was weighed.

ORD = ORDer in which the sexual was weighed.

COL = COLony (ie., nest) identification number, just as in Appendix 2.

SX = SeX of sexual; 0 = male; 1 = female.

CN = CoNdition of sexual, a code number as defined in Table A3.1 above.

DW = Dry Weight in micrograms.

The TUB numbers for the early and late sexuals for both batches are shown in Table A3.3 below. Counting errors resulted in discrepancies between the TUB numbers and the numbers of sexuals actually weighed. For example, only 535 early sexuals were weighed in batch #1 and yet the TUB numbers for these sexuals ranged from 1 to 538. These discrepancies are explained in the preliminary to each batch.

**Table A3.3 TUB numbers for the early and late sexuals in each batch (see Table A3.2 for the numbers actually weighed).**

| Batch | Date nests were collected (1992) | TUB numbers Early sexuals | Late sexuals |
|---|---|---|---|
| #1 | 20 June | 1-538 | 539-974 |
| | 4 July | 1-314 | 315-331 |
| | 20 July | 332-657 | 658-684 |
| #2 | 8 August | 685 | - |
| | 29 August | 686 | 687 |
| | 17 Sept. | 688 | - |

The data for batch #1 are shown below. Unfortunately, three TUB numbers (455, 477 and 522) were accidentally omitted, and, of the ORD numbers, 9 were duplicated (101, 283, 315, 325, 342, 345, 463, 916 and 934) and 5 omitted (106, 150, 320, 375 and 394). This explains the discrepancy between the final TUB number, 974, and the number of sexuals actually weighed, 971; since (974 - 3) = (967 + 9 - 5) = 971, where 967 was the maximum value of ORD.

| TUB | ORD | COL | SX | CN | DW |
|---|---|---|---|---|---|
| 1 | 530 | 143 | 1 | 1 | 631 |
| 2 | 854 | 143 | 0 | 1 | 212 |
| 3 | 691 | 143 | 1 | 1 | 623 |
| 4 | 946 | 143 | 1 | 1 | 555 |
| 5 | 276 | 143 | 0 | 1 | 196 |
| 6 | 273 | 143 | 1 | 1 | 568 |
| 7 | 753 | 143 | 1 | 5 | 664 |
| 8 | 74 | 143 | 1 | 1 | 594 |
| 9 | 712 | 143 | 1 | 1 | 600 |
| 10 | 66 | 143 | 1 | 1 | 693 |
| 11 | 365 | 143 | 1 | 1 | 622 |
| 12 | 822 | 143 | 1 | 1 | 564 |
| 13 | 142 | 143 | 1 | 1 | 624 |
| 14 | 761 | 143 | 1 | 1 | 513 |
| 15 | 936 | 143 | 1 | 2 | 587 |
| 16 | 664 | 143 | 1 | 1 | 616 |
| 17 | 638 | 143 | 1 | 1 | 633 |
| 18 | 809 | 150 | 1 | 1 | 634 |
| 19 | 339 | 150 | 1 | 1 | 610 |
| 20 | 250 | 150 | 1 | 1 | 687 |
| 21 | 532 | 150 | 1 | 1 | 595 |
| 22 | 53 | 150 | 1 | 1 | 553 |
| 23 | 261 | 150 | 1 | 1 | 622 |
| 24 | 89 | 150 | 0 | 1 | 253 |
| 25 | 860 | 150 | 0 | 2 | 229 |
| 26 | 116 | 150 | 1 | 1 | 599 |
| 27 | 110 | 150 | 1 | 1 | 567 |
| 28 | 488 | 150 | 1 | 3 | 595 |
| 29 | 147 | 150 | 0 | 1 | 186 |
| 30 | 426 | 150 | 1 | 1 | 567 |
| 31 | 655 | 150 | 1 | 1 | 526 |
| 32 | 951 | 150 | 1 | 2 | 594 |
| 33 | 76 | 150 | 1 | 1 | 683 |
| 34 | 430 | 150 | 0 | 2 | 223 |
| 35 | 647 | 150 | 1 | 1 | 589 |
| 36 | 386 | 150 | 0 | 1 | 194 |
| 37 | 789 | 152 | 1 | 2 | 468 |
| 38 | 893 | 137 | 0 | 1 | 159 |
| 39 | 470 | 137 | 0 | 1 | 168 |
| 40 | * | 137 | 0 | 1 | 167 |
| 41 | 903 | 137 | 0 | 1 | 141 |
| 42 | 525 | 137 | 0 | 1 | 146 |
| 43 | 302 | 137 | 0 | 1 | 137 |
| 44 | 573 | 137 | 0 | 1 | 141 |
| 45 | 794 | 137 | 0 | 1 | 112 |
| 46 | 653 | 137 | 0 | 1 | 141 |
| 47 | 25 | 137 | 0 | 1 | 145 |
| 48 | 821 | 137 | 0 | 1 | 131 |
| 49 | 607 | 164 | 0 | 3 | 210 |
| 50 | 849 | 164 | 0 | 1 | 174 |
| 51 | 441 | 164 | 0 | 1 | 197 |
| 52 | 895 | 164 | 0 | 1 | 194 |
| 53 | 803 | 164 | 0 | 1 | 176 |
| 54 | 768 | 164 | 0 | 1 | 193 |
| 55 | 194 | 164 | 0 | 1 | 159 |
| 56 | 514 | 164 | 0 | 1 | 191 |
| 57 | 956 | 164 | 0 | 1 | 158 |
| 58 | 502 | 164 | 1 | 1 | 666 |
| 59 | 831 | 164 | 0 | 5 | 181 |
| 60 | 236 | 164 | 0 | 1 | 193 |
| 61 | 112 | 164 | 0 | 1 | 176 |
| 62 | 880 | 164 | 1 | 1 | 717 |
| 63 | 251 | 164 | 1 | 1 | 722 |
| 64 | 669 | 164 | 0 | 1 | 159 |
| 65 | 528 | 164 | 0 | 1 | 199 |
| 66 | 606 | 164 | 0 | 1 | 171 |
| 67 | 456 | 164 | 0 | 1 | 136 |
| 68 | 604 | 164 | 0 | 1 | 178 |
| 69 | 830 | 164 | 0 | 1 | 178 |
| 70 | 862 | 164 | 0 | 1 | 187 |
| 71 | 421 | 164 | 1 | 1 | 713 |
| 72 | 927 | 164 | 0 | 1 | 207 |
| 73 | 383 | 164 | 0 | 1 | 164 |
| 74 | 171 | 164 | 0 | 5 | 174 |
| 75 | 449 | 164 | 0 | 1 | 191 |
| 76 | 679 | 164 | 1 | 1 | 789 |
| 77 | 945 | 164 | 0 | 1 | 174 |
| 78 | 652 | 164 | 0 | 1 | 161 |
| 79 | 529 | 164 | 1 | 1 | 722 |
| 80 | 473 | 164 | 0 | 1 | 239 |
| 81 | 230 | 164 | 0 | 1 | 157 |
| 82 | 411 | 164 | 0 | 1 | 198 |
| 83 | 557 | 164 | 0 | 1 | 175 |
| 84 | 331 | 164 | 0 | 1 | 166 |
| 85 | 588 | 164 | 0 | 3 | 143 |
| 86 | 433 | 164 | 1 | 1 | 683 |
| 87 | 919 | 164 | 1 | 1 | 624 |
| 88 | 519 | 164 | 0 | 1 | 190 |
| 89 | 52 | 164 | 0 | 1 | 129 |
| 90 | 97 | 164 | 0 | 1 | 131 |
| 91 | 892 | 164 | 0 | 1 | 185 |
| 92 | 694 | 164 | 1 | 1 | 715 |
| 93 | 480 | 164 | 0 | 1 | 179 |
| 94 | 889 | 164 | 0 | 1 | 173 |
| 95 | 80 | 164 | 0 | 1 | 149 |
| 96 | 127 | 164 | 0 | 1 | 147 |
| 97 | 311 | 164 | 1 | 1 | 785 |
| 98 | 786 | 164 | 1 | 1 | 701 |
| 99 | 482 | 164 | 0 | 1 | 180 |
| 100 | 785 | 164 | 0 | 1 | 190 |
| 101 | 714 | 164 | 0 | 1 | 166 |
| 102 | 911 | 164 | 1 | 1 | 736 |
| 103 | 18 | 164 | 0 | 1 | 164 |
| 104 | 913 | 164 | 0 | 1 | 162 |
| 105 | 434 | 164 | 0 | 1 | 167 |
| 106 | 864 | 164 | 0 | 1 | 178 |
| 107 | 643 | 164 | 0 | 1 | 218 |
| 108 | 920 | 164 | 0 | 3 | 192 |
| 109 | 569 | 164 | 1 | 1 | 600 |
| 110 | 466 | 164 | 1 | 1 | 674 |
| 111 | 835 | 164 | 0 | 1 | 152 |
| 112 | 363 | 164 | 0 | 1 | 209 |
| 113 | 583 | 164 | 1 | 1 | 731 |
| 114 | 633 | 164 | 0 | 1 | 142 |
| 115 | 90 | 164 | 0 | 1 | 169 |

| | | | | | |
|---|---|---|---|---|---|
| 116 | 521 | 164 | 0 | 1 | 155 |
| 117 | 625 | 164 | 0 | 1 | 163 |
| 118 | 182 | 164 | 0 | 1 | 168 |
| 119 | 283 | 164 | 0 | 6 | 198 |
| 120 | 232 | 164 | 0 | 1 | 196 |
| 121 | 967 | 149 | 1 | 3 | 532 |
| 122 | 848 | 149 | 1 | 1 | 563 |
| 123 | 865 | 149 | 1 | 1 | 518 |
| 124 | 948 | 149 | 1 | 1 | 538 |
| 125 | 705 | 149 | 1 | 1 | 509 |
| 126 | 72 | 149 | 1 | 1 | 553 |
| 127 | 286 | 149 | 1 | 1 | 535 |
| 128 | 725 | 149 | 1 | 1 | 492 |
| 129 | 316 | 149 | 1 | 1 | 547 |
| 130 | 767 | 149 | 1 | 1 | 516 |
| 131 | 605 | 160 | 1 | 1 | 599 |
| 132 | 68 | 160 | 0 | 1 | 191 |
| 133 | 757 | 160 | 0 | 1 | 162 |
| 134 | 503 | 160 | 0 | 1 | 151 |
| 135 | 39 | 160 | 0 | 1 | 222 |
| 136 | 416 | 151 | 0 | 1 | 115 |
| 137 | 727 | 154 | 0 | 1 | 154 |
| 138 | 371 | 140 | 0 | 1 | 163 |
| 139 | 306 | 140 | 0 | 1 | 142 |
| 140 | 281 | 156 | 0 | 1 | 196 |
| 141 | 897 | 153 | 0 | 1 | 126 |
| 142 | 740 | 153 | 0 | 1 | 131 |
| 143 | 125 | 159 | 0 | 1 | 148 |
| 144 | 558 | 163 | 0 | 3 | 172 |
| 145 | 782 | 163 | 0 | 1 | 169 |
| 146 | 216 | 163 | 1 | 1 | 592 |
| 147 | 741 | 163 | 1 | 1 | 620 |
| 148 | 95 | 163 | 1 | 1 | 669 |
| 149 | 674 | 163 | 1 | 1 | 634 |
| 150 | 199 | 163 | 1 | 3 | 677 |
| 151 | 378 | 163 | 1 | 2 | 621 |
| 152 | 132 | 163 | 1 | 1 | 581 |
| 153 | 137 | 163 | 1 | 1 | 656 |
| 154 | 841 | 163 | 1 | 1 | 597 |
| 155 | 680 | 147 | 0 | 1 | 145 |
| 156 | 107 | 147 | 0 | 1 | 169 |
| 157 | 814 | 147 | 0 | 1 | 150 |
| 158 | 59 | 139 | 0 | 1 | 119 |
| 159 | 734 | 139 | 0 | 1 | 120 |
| 160 | 752 | 139 | 0 | 1 | 99 |
| 161 | 184 | 161 | 0 | 1 | 174 |
| 162 | 101 | 161 | 0 | 2 | 164 |
| 163 | 931 | 161 | 0 | 2 | 229 |
| 164 | 684 | 161 | 0 | 1 | 170 |
| 165 | 392 | 161 | 0 | 1 | 164 |
| 166 | 527 | 161 | 0 | 1 | 155 |
| 167 | 139 | 161 | 0 | 1 | 213 |
| 168 | 246 | 161 | 0 | 1 | 183 |
| 169 | 382 | 161 | 0 | 1 | 178 |
| 170 | 78 | 161 | 0 | 1 | 179 |
| 171 | 866 | 161 | 0 | 1 | 151 |
| 172 | 645 | 161 | 0 | 1 | 165 |
| 173 | 239 | 161 | 0 | 2 | 224 |
| 174 | 14 | 161 | 0 | 1 | 164 |
| 175 | 724 | 161 | 0 | 6 | 143 |
| 176 | 160 | 161 | 0 | 1 | 161 |
| 177 | 412 | 161 | 0 | 1 | 171 |
| 178 | 326 | 161 | 0 | 1 | 165 |
| 179 | 33 | 136 | 1 | 1 | 541 |
| 180 | 808 | 136 | 1 | 1 | 764 |
| 181 | 471 | 136 | 1 | 3 | 617 |
| 182 | 717 | 136 | 1 | 1 | 673 |
| 183 | 839 | 136 | 1 | 1 | 645 |
| 184 | 225 | 136 | 0 | 1 | 198 |
| 185 | 419 | 136 | 1 | 1 | 639 |
| 186 | 440 | 136 | 1 | 1 | 592 |
| 187 | 737 | 136 | 1 | 1 | 577 |
| 188 | 746 | 136 | 0 | 1 | 203 |
| 189 | 551 | 136 | 1 | 1 | 623 |
| 190 | 817 | 136 | 1 | 1 | 563 |
| 191 | 642 | 136 | 1 | 1 | 656 |
| 192 | 833 | 136 | 1 | 3 | 717 |
| 193 | 64 | 136 | 1 | 1 | 641 |
| 194 | 629 | 136 | 0 | 1 | 180 |
| 195 | * | 136 | 1 | 1 | 719 |
| 196 | 253 | 136 | 1 | 1 | 666 |
| 197 | 907 | 136 | 1 | 1 | 577 |
| 198 | 730 | 136 | 0 | 1 | 178 |
| 199 | 309 | 165 | 0 | 1 | 150 |
| 200 | 57 | 165 | 0 | 1 | 154 |
| 201 | 755 | 165 | 0 | 1 | 157 |
| 202 | 372 | 165 | 0 | 1 | 136 |
| 203 | 693 | 165 | 0 | 1 | 140 |
| 204 | 695 | 165 | 1 | 1 | 723 |
| 205 | 294 | 165 | 0 | 1 | 200 |
| 206 | 552 | 165 | 1 | 1 | 721 |
| 207 | 404 | 165 | 0 | 1 | 192 |
| 208 | 210 | 165 | 0 | 5 | 170 |
| 209 | 498 | 165 | 1 | 1 | 691 |
| 210 | 534 | 165 | 0 | 1 | 187 |
| 211 | 330 | 165 | 0 | 1 | 164 |
| 212 | 957 | 165 | 1 | 1 | 697 |
| 213 | 494 | 165 | 1 | 1 | 614 |
| 214 | 291 | 165 | 0 | 1 | 168 |
| 215 | 360 | 165 | 0 | 1 | 159 |
| 216 | 464 | 165 | 0 | 1 | 167 |
| 217 | 663 | 165 | 0 | 1 | 141 |
| 218 | 916 | 165 | 0 | 1 | 184 |
| 219 | 584 | 165 | 0 | 1 | 130 |
| 220 | 939 | 165 | 0 | 5 | 137 |
| 221 | 934 | 165 | 0 | 1 | 170 |
| 222 | 733 | 165 | 1 | 1 | 763 |
| 223 | 228 | 165 | 0 | 1 | 163 |
| 224 | 888 | 165 | 1 | 1 | 708 |
| 225 | 75 | 165 | 0 | 1 | 98 |
| 226 | 912 | 165 | 1 | 1 | 758 |
| 227 | 896 | 165 | 1 | 1 | 613 |
| 228 | 879 | 165 | 0 | 1 | 144 |
| 229 | 868 | 165 | 1 | 3 | 605 |
| 230 | 673 | 165 | 0 | 1 | 149 |
| 231 | 658 | 165 | 1 | 1 | 616 |
| 232 | 204 | 165 | 0 | 1 | 129 |
| 233 | 349 | 165 | 0 | 1 | 124 |
| 234 | 353 | 165 | 0 | 1 | 183 |
| 235 | 355 | 165 | 0 | 1 | 185 |
| 236 | 218 | 165 | 1 | 1 | 775 |
| 237 | 474 | 165 | 0 | 2 | 155 |
| 238 | 304 | 165 | 0 | 1 | 122 |
| 239 | 772 | 165 | 0 | 1 | 202 |
| 240 | 101 | 165 | 0 | 1 | 166 |
| 241 | 453 | 165 | 1 | 1 | 658 |
| 242 | 950 | 165 | 0 | 2 | 126 |
| 243 | 390 | 165 | 0 | 1 | 181 |
| 244 | 325 | 165 | 0 | 1 | 175 |
| 245 | 917 | 165 | 0 | 1 | 124 |
| 246 | 191 | 165 | 1 | 1 | 679 |
| 247 | 207 | 165 | 0 | 1 | 161 |
| 248 | 965 | 165 | 0 | 1 | 160 |
| 249 | 536 | 165 | 0 | 1 | 163 |
| 250 | 797 | 165 | 0 | 1 | 138 |
| 251 | 92 | 165 | 1 | 1 | 624 |
| 252 | 876 | 165 | 0 | 1 | 127 |
| 253 | 215 | 165 | 1 | 1 | 576 |
| 254 | 133 | 165 | 0 | 1 | 178 |
| 255 | 179 | 165 | 0 | 1 | 150 |
| 256 | 493 | 165 | 0 | 1 | 174 |
| 257 | 804 | 165 | 0 | 1 | 152 |
| 258 | 87 | 165 | 1 | 1 | 746 |
| 259 | 546 | 165 | 0 | 1 | 178 |
| 260 | 923 | 165 | 0 | 2 | 166 |
| 261 | 555 | 165 | 0 | 1 | 167 |
| 262 | 352 | 165 | 0 | 1 | 180 |
| 263 | 267 | 165 | 0 | 1 | 134 |
| 264 | 599 | 165 | 1 | 1 | 590 |
| 265 | 389 | 165 | 0 | 1 | 121 |
| 266 | 571 | 165 | 0 | 2 | 169 |
| 267 | 828 | 165 | 0 | 1 | 188 |
| 268 | 479 | 142 | 0 | 1 | 154 |
| 269 | 115 | 142 | 0 | 1 | 136 |
| 270 | 88 | 142 | 0 | 1 | 137 |
| 271 | 315 | 142 | 0 | 1 | 134 |
| 272 | 175 | 142 | 0 | 1 | 134 |
| 273 | 62 | 142 | 0 | 1 | 154 |
| 274 | 816 | 142 | 0 | 1 | 155 |
| 275 | 636 | 142 | 1 | 1 | 595 |
| 276 | 941 | 142 | 0 | 1 | 159 |
| 277 | 462 | 142 | 1 | 1 | 662 |
| 278 | 689 | 142 | 0 | 1 | 164 |
| 279 | 431 | 142 | 1 | 1 | 664 |
| 280 | 556 | 142 | 0 | 1 | 138 |
| 281 | 902 | 142 | 0 | 1 | 161 |
| 282 | 934 | 142 | 0 | 2 | 184 |
| 283 | 263 | 142 | 0 | 1 | 147 |
| 284 | 30 | 142 | 1 | 1 | 651 |
| 285 | 916 | 142 | 1 | 1 | 697 |
| 286 | 323 | 142 | 0 | 1 | 173 |

| | | | | | |
|---|---|---|---|---|---|
| 287 | 632 | 142 | 0 | 1 | 147 |
| 288 | 193 | 142 | 0 | 1 | 149 |
| 289 | 144 | 142 | 1 | 1 | 651 |
| 290 | 845 | 142 | 1 | 1 | 717 |
| 291 | 269 | 142 | 1 | 1 | 688 |
| 292 | 955 | 142 | 1 | 1 | 634 |
| 293 | 614 | 142 | 0 | 1 | 149 |
| 294 | 103 | 142 | 1 | 1 | 619 |
| 295 | 70 | 142 | 1 | 1 | 671 |
| 296 | 548 | 142 | 0 | 1 | 168 |
| 297 | 732 | 142 | 0 | 1 | 153 |
| 298 | 91 | 142 | 1 | 1 | 693 |
| 299 | 335 | 142 | 0 | 1 | 144 |
| 300 | 509 | 142 | 1 | 1 | 610 |
| 301 | 802 | 142 | 0 | 1 | 149 |
| 302 | 104 | 142 | 0 | 1 | 145 |
| 303 | 938 | 142 | 0 | 1 | 161 |
| 304 | 403 | 142 | 0 | 1 | 157 |
| 305 | 409 | 142 | 0 | 1 | 146 |
| 306 | 463 | 142 | 0 | 1 | 147 |
| 307 | 754 | 142 | 0 | 1 | 151 |
| 308 | 443 | 142 | 0 | 1 | 161 |
| 309 | 235 | 142 | 0 | 1 | 132 |
| 310 | 586 | 142 | 0 | 1 | 188 |
| 311 | 249 | 142 | 1 | 1 | 694 |
| 312 | 703 | 142 | 1 | 1 | 700 |
| 313 | 771 | 142 | 0 | 5 | 130 |
| 314 | 762 | 142 | 1 | 1 | 630 |
| 315 | 882 | 142 | 1 | 1 | 653 |
| 316 | 180 | 142 | 1 | 1 | 651 |
| 317 | 838 | 142 | 1 | 1 | 607 |
| 318 | 777 | 142 | 0 | 1 | 166 |
| 319 | 678 | 142 | 0 | 1 | 158 |
| 320 | 81 | 142 | 1 | 1 | 617 |
| 321 | 242 | 142 | 0 | 1 | 156 |
| 322 | 793 | 142 | 0 | 1 | 157 |
| 323 | 487 | 142 | 1 | 1 | 689 |
| 324 | 432 | 142 | 0 | 1 | 153 |
| 325 | 535 | 142 | 0 | 3 | 158 |
| 326 | 370 | 142 | 1 | 1 | 597 |
| 327 | 520 | 142 | 0 | 2 | 144 |
| 328 | 863 | 142 | 0 | 1 | 168 |
| 329 | 744 | 142 | 0 | 1 | 134 |
| 330 | 262 | 142 | 0 | 1 | 150 |
| 331 | 587 | 142 | 0 | 1 | 146 |
| 332 | 729 | 142 | 0 | 1 | 147 |
| 333 | 374 | 142 | 0 | 1 | 151 |
| 334 | 166 | 142 | 0 | 3 | 164 |
| 335 | 477 | 142 | 0 | 1 | 126 |
| 336 | 108 | 142 | 1 | 1 | 636 |
| 337 | 164 | 142 | 0 | 1 | 154 |
| 338 | 178 | 142 | 0 | 1 | 145 |
| 339 | * | 145 | 1 | 1 | 620 |
| 340 | 272 | 145 | 1 | 1 | 570 |
| 341 | 873 | 145 | 1 | 1 | 568 |
| 342 | 428 | 145 | 1 | 1 | 573 |
| 343 | 937 | 145 | 1 | 2 | 528 |
| 344 | 186 | 145 | 1 | 3 | 551 |
| 345 | 702 | 145 | 1 | 2 | 597 |
| 346 | 245 | 145 | 1 | 1 | 657 |
| 347 | 639 | 145 | 1 | 1 | 559 |
| 348 | 168 | 145 | 1 | 1 | 524 |
| 349 | 465 | 145 | 1 | 1 | 500 |
| 350 | 685 | 145 | 1 | 1 | 636 |
| 351 | 56 | 145 | 1 | 1 | 611 |
| 352 | 446 | 145 | 1 | 1 | 660 |
| 353 | 501 | 145 | 1 | 1 | 546 |
| 354 | 759 | 145 | 1 | 1 | 596 |
| 355 | 770 | 145 | 1 | 1 | 553 |
| 356 | 780 | 145 | 1 | 1 | 567 |
| 357 | 721 | 145 | 1 | 1 | 536 |
| 358 | 661 | 145 | 1 | 1 | 645 |
| 359 | 265 | 145 | 1 | 1 | 554 |
| 360 | 624 | 145 | 1 | 1 | 607 |
| 361 | 875 | 145 | 1 | 1 | 584 |
| 362 | 188 | 145 | 1 | 1 | 572 |
| 363 | 834 | 145 | 1 | 1 | 553 |
| 364 | 84 | 145 | 1 | 1 | 570 |
| 365 | 16 | 144 | 0 | 2 | 148 |
| 366 | 898 | 144 | 0 | 1 | 170 |
| 367 | 621 | 144 | 1 | 1 | 505 |
| 368 | 539 | 144 | 0 | 1 | 167 |
| 369 | 380 | 144 | 0 | 1 | 141 |
| 370 | 844 | 144 | 0 | 1 | 164 |
| 371 | 840 | 144 | 0 | 1 | 131 |
| 372 | 469 | 144 | 0 | 1 | 114 |
| 373 | 623 | 144 | 1 | 1 | 514 |
| 374 | 314 | 144 | 1 | 1 | 631 |
| 375 | 615 | 144 | 0 | 1 | 153 |
| 376 | 37 | 144 | 0 | 1 | 142 |
| 377 | 622 | 144 | 0 | 1 | 118 |
| 378 | 631 | 144 | 0 | 1 | 148 |
| 379 | 515 | 144 | 0 | 1 | 149 |
| 380 | 51 | 144 | 0 | 1 | 137 |
| 381 | 96 | 144 | 0 | 1 | 156 |
| 382 | * | 144 | 0 | 1 | 139 |
| 383 | 657 | 144 | 0 | 1 | 112 |
| 384 | 357 | 144 | 1 | 1 | 475 |
| 385 | 491 | 144 | 1 | 1 | 552 |
| 386 | 843 | 144 | 1 | 1 | 584 |
| 387 | 914 | 144 | 1 | 1 | 520 |
| 388 | 791 | 144 | 0 | 1 | 146 |
| 389 | 222 | 144 | 1 | 1 | 509 |
| 390 | 393 | 144 | 0 | 1 | 127 |
| 391 | 775 | 144 | 0 | 1 | 129 |
| 392 | 27 | 144 | 0 | 1 | 151 |
| 393 | 397 | 144 | 0 | 1 | 139 |
| 394 | 313 | 144 | 1 | 1 | 580 |
| 395 | 405 | 144 | 0 | 1 | 151 |
| 396 | 458 | 144 | 1 | 1 | 508 |
| 397 | 708 | 144 | 1 | 1 | 580 |
| 398 | 450 | 144 | 0 | 1 | 133 |
| 399 | 562 | 144 | 0 | 2 | 157 |
| 400 | 192 | 144 | 1 | 1 | 514 |
| 401 | 332 | 144 | 1 | 1 | 526 |
| 402 | 158 | 144 | 0 | 1 | 112 |
| 403 | 921 | 144 | 0 | 1 | 160 |
| 404 | 161 | 144 | 0 | 1 | 146 |
| 405 | 958 | 144 | 1 | 1 | 512 |
| 406 | 58 | 144 | 0 | 1 | 142 |
| 407 | 427 | 144 | 1 | 1 | 574 |
| 408 | 170 | 144 | 0 | 1 | 134 |
| 409 | 34 | 144 | 0 | 1 | 136 |
| 410 | 812 | 144 | 0 | 1 | 142 |
| 411 | 784 | 144 | 1 | 1 | 559 |
| 412 | 238 | 144 | 0 | 1 | 119 |
| 413 | 696 | 144 | 0 | 5 | 145 |
| 414 | 887 | 144 | 0 | 2 | 188 |
| 415 | 776 | 144 | 0 | 1 | 139 |
| 416 | 63 | 144 | 0 | 1 | 133 |
| 417 | 43 | 144 | 0 | 1 | 102 |
| 418 | 750 | 144 | 0 | 1 | 136 |
| 419 | 350 | 144 | 0 | 1 | 141 |
| 420 | 874 | 144 | 1 | 1 | 588 |
| 421 | 666 | 144 | 0 | 1 | 135 |
| 422 | 500 | 144 | 0 | 1 | 135 |
| 423 | 671 | 144 | 1 | 1 | 589 |
| 424 | 960 | 144 | 0 | 1 | 146 |
| 425 | 329 | 144 | 0 | 3 | 138 |
| 426 | 438 | 144 | 0 | 1 | 116 |
| 427 | 736 | 144 | 0 | 1 | 143 |
| 428 | 156 | 144 | 0 | 1 | 127 |
| 429 | 577 | 144 | 0 | 1 | 150 |
| 430 | 574 | 144 | 0 | 1 | 144 |
| 431 | 857 | 144 | 0 | 1 | 123 |
| 432 | 295 | 144 | 0 | 1 | 146 |
| 433 | 935 | 144 | 0 | 1 | 144 |
| 434 | 475 | 144 | 0 | 1 | 150 |
| 435 | 384 | 144 | 0 | 1 | 149 |
| 436 | 358 | 144 | 0 | 1 | 130 |
| 437 | 728 | 144 | 1 | 1 | 519 |
| 438 | 719 | 144 | 0 | 1 | 135 |
| 439 | 582 | 144 | 0 | 1 | 119 |
| 440 | 853 | 144 | 0 | 1 | 142 |
| 441 | 177 | 144 | 0 | 1 | 133 |
| 442 | 928 | 144 | 0 | 1 | 140 |
| 443 | 559 | 144 | 0 | 1 | 150 |
| 444 | 361 | 144 | 1 | 1 | 526 |
| 445 | 953 | 144 | 0 | 1 | 136 |
| 446 | 439 | 144 | 0 | 1 | 154 |
| 447 | 756 | 144 | 1 | 1 | 530 |
| 448 | 17 | 144 | 0 | 1 | 157 |
| 449 | 589 | 144 | 0 | 1 | 142 |
| 450 | 799 | 144 | 0 | 2 | 128 |
| 451 | 827 | 144 | 0 | 1 | 166 |
| 452 | 113 | 144 | 0 | 1 | 139 |
| 453 | 270 | 144 | 0 | 1 | 134 |
| 454 | 566 | 144 | 0 | 1 | 130 |
| * | * | * | * | * | * |
| 456 | 489 | 144 | 0 | 1 | 121 |
| 457 | 635 | 144 | 0 | 1 | 132 |

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|---|---|---|---|---|---|
| 458 | 343 | 144 | 0 | 1 | 141 |
| 459 | 616 | 144 | 0 | 1 | 130 |
| 460 | 561 | 144 | 0 | 1 | 126 |
| 461 | 415 | 144 | 0 | 1 | 140 |
| 462 | 157 | 144 | 0 | 1 | 153 |
| 463 | 336 | 144 | 0 | 1 | 140 |
| 464 | 602 | 144 | 0 | 1 | 150 |
| 465 | 617 | 144 | 1 | 1 | 521 |
| 466 | 593 | 144 | 0 | 1 | 154 |
| 467 | 846 | 144 | 1 | 1 | 577 |
| 468 | 296 | 148 | 0 | 5 | 180 |
| 469 | 505 | 148 | 1 | 1 | 670 |
| 470 | 836 | 148 | 0 | 1 | 186 |
| 471 | 256 | 148 | 1 | 1 | 598 |
| 472 | 610 | 148 | 1 | 1 | 662 |
| 473 | 774 | 148 | 1 | 1 | 660 |
| 474 | 292 | 148 | 0 | 1 | 165 |
| 475 | 932 | 148 | 0 | 1 | 222 |
| 476 | 472 | 148 | 0 | 1 | 194 |
| * | * | * | * | * | * |
| 478 | 289 | 148 | 1 | 1 | 611 |
| 479 | 111 | 148 | 0 | 1 | 210 |
| 480 | 93 | 148 | 1 | 1 | 699 |
| 481 | 723 | 148 | 1 | 1 | 635 |
| 482 | 226 | 148 | 1 | 1 | 668 |
| 483 | 769 | 148 | 0 | 1 | 175 |
| 484 | 952 | 148 | 1 | 1 | 583 |
| 485 | 424 | 148 | 0 | 1 | 172 |
| 486 | 346 | 148 | 0 | 1 | 184 |
| 487 | 278 | 148 | 1 | 1 | 665 |
| 488 | 681 | 148 | 0 | 1 | 154 |
| 489 | 591 | 148 | 1 | 5 | 615 |
| 490 | 648 | 148 | 0 | 1 | 158 |
| 491 | 601 | 148 | 1 | 1 | 655 |
| 492 | 455 | 148 | 0 | 1 | 173 |
| 493 | 209 | 148 | 0 | 1 | 192 |
| 494 | 540 | 148 | 0 | 1 | 193 |
| 495 | 203 | 148 | 0 | 1 | 180 |
| 496 | 869 | 148 | 0 | 1 | 204 |
| 497 | 641 | 148 | 1 | 1 | 760 |
| 498 | 942 | 148 | 1 | 1 | 623 |
| 499 | 486 | 148 | 1 | 1 | 669 |
| 500 | 305 | 148 | 1 | 1 | 716 |
| 501 | 544 | 148 | 0 | 1 | 170 |
| 502 | 22 | 148 | 0 | 1 | 191 |
| 503 | 457 | 148 | 0 | 1 | 200 |
| 504 | 603 | 148 | 1 | 1 | 618 |
| 505 | 345 | 148 | 0 | 1 | 192 |
| 506 | 947 | 148 | 0 | 2 | 187 |
| 507 | 122 | 148 | 0 | 1 | 181 |
| 508 | 285 | 148 | 1 | 1 | 660 |
| 509 | 148 | 148 | 0 | 1 | 157 |
| 510 | 44 | 148 | 1 | 1 | 614 |
| 511 | 255 | 148 | 1 | 1 | 669 |
| 512 | 795 | 148 | 1 | 1 | 654 |
| 513 | 283 | 148 | 1 | 1 | 663 |
| 514 | 387 | 148 | 1 | 1 | 637 |
| 515 | 676 | 148 | 0 | 1 | 195 |
| 516 | 765 | 148 | 1 | 1 | 654 |
| 517 | 32 | 148 | 0 | 1 | 220 |
| 518 | 459 | 148 | 1 | 1 | 666 |
| 519 | 651 | 148 | 0 | 1 | 160 |
| 520 | 800 | 148 | 0 | 1 | 168 |
| 521 | 751 | 148 | 0 | 1 | 212 |
| * | * | * | * | * | * |
| 523 | 682 | 148 | 1 | 1 | 695 |
| 524 | 788 | 148 | 0 | 1 | 174 |
| 525 | 40 | 148 | 0 | 1 | 146 |
| 526 | 640 | 148 | 0 | 1 | 186 |
| 527 | 735 | 148 | 0 | 1 | 210 |
| 528 | 954 | 148 | 0 | 1 | 197 |
| 529 | * | 148 | 0 | 1 | 173 |
| 530 | 634 | 148 | 1 | 1 | 621 |
| 531 | 858 | 148 | 1 | 2 | 623 |
| 532 | 143 | 148 | 0 | 1 | 185 |
| 533 | 12 | 148 | 0 | 1 | 212 |
| 534 | 670 | 148 | 0 | 1 | 151 |
| 535 | 176 | 148 | 0 | 1 | 176 |
| 536 | 460 | 148 | 0 | 2 | 164 |
| 537 | 837 | 148 | 0 | 1 | 172 |
| 538 | 925 | 148 | 0 | 2 | 201 |
| 539 | 463 | 144 | 0 | 2 | 156 |
| 540 | 284 | 144 | 0 | 5 | 124 |
| 541 | 590 | 144 | 0 | 1 | 139 |
| 542 | 715 | 144 | 0 | 1 | 143 |
| 543 | 495 | 144 | 0 | 1 | 155 |
| 544 | 318 | 144 | 0 | 1 | 149 |
| 545 | 290 | 144 | 0 | 1 | 136 |
| 546 | 533 | 144 | 0 | 1 | 153 |
| 547 | 408 | 144 | 0 | 1 | 151 |
| 548 | 637 | 144 | 0 | 1 | 146 |
| 549 | 327 | 144 | 0 | 1 | 153 |
| 550 | 221 | 144 | 0 | 5 | 130 |
| 551 | 690 | 144 | 0 | 1 | 184 |
| 552 | 620 | 144 | 0 | 1 | 144 |
| 553 | 649 | 144 | 0 | 2 | 158 |
| 554 | 855 | 144 | 0 | 1 | 164 |
| 555 | 20 | 144 | 0 | 1 | 169 |
| 556 | 595 | 144 | 0 | 1 | 148 |
| 557 | 220 | 144 | 0 | 1 | 193 |
| 558 | 45 | 144 | 0 | 5 | 161 |
| 559 | 490 | 144 | 0 | 1 | 173 |
| 560 | 687 | 144 | 0 | 1 | 137 |
| 561 | 545 | 144 | 0 | 1 | 163 |
| 562 | 219 | 144 | 0 | 1 | 155 |
| 563 | 720 | 144 | 0 | 1 | 174 |
| 564 | 881 | 144 | 1 | 5 | 458 |
| 565 | 859 | 144 | 0 | 1 | 136 |
| 566 | 575 | 144 | 1 | 1 | 570 |
| 567 | 796 | 144 | 1 | 1 | 550 |
| 568 | 467 | 144 | 0 | 1 | 167 |
| 569 | 447 | 144 | 0 | 1 | 156 |
| 570 | 758 | 144 | 0 | 2 | 164 |
| 571 | 85 | 144 | 0 | 1 | 170 |
| 572 | 102 | 142 | 1 | 5 | 497 |
| 573 | 274 | 142 | 0 | 5 | 108 |
| 574 | 154 | 142 | 0 | 5 | 117 |
| 575 | 748 | 142 | 0 | 5 | 105 |
| 576 | 512 | 142 | 0 | 1 | 125 |
| 577 | 585 | 142 | 0 | 5 | 87 |
| 578 | 910 | 142 | 0 | 1 | 117 |
| 579 | 42 | 142 | 0 | 5 | 106 |
| 580 | 280 | 142 | 0 | 1 | 107 |
| 581 | 510 | 142 | 0 | 5 | 110 |
| 582 | 300 | 142 | 0 | 5 | 119 |
| 583 | 362 | 142 | 0 | 1 | 111 |
| 584 | 890 | 142 | 0 | 1 | 109 |
| 585 | 134 | 142 | 1 | 1 | 696 |
| 586 | 152 | 142 | 0 | 1 | 110 |
| 587 | 282 | 142 | 0 | 5 | 117 |
| 588 | 366 | 142 | 1 | 5 | 577 |
| 589 | 600 | 142 | 0 | 1 | 116 |
| 590 | 259 | 142 | 0 | 1 | 134 |
| 591 | 185 | 142 | 0 | 1 | 131 |
| 592 | 15 | 142 | 0 | 1 | 126 |
| 593 | 851 | 142 | 0 | 1 | 134 |
| 594 | 943 | 142 | 0 | 5 | 109 |
| 595 | 325 | 142 | 0 | 1 | 135 |
| 596 | 543 | 142 | 0 | 5 | 112 |
| 597 | 824 | 139 | 0 | 1 | 105 |
| 598 | 966 | 139 | 0 | 1 | 116 |
| 599 | 341 | 139 | 0 | 1 | 77 |
| 600 | 499 | 139 | 0 | 5 | 102 |
| 601 | * | 139 | 0 | 1 | 111 |
| 602 | 213 | 139 | 0 | 1 | 105 |
| 603 | 345 | 139 | 0 | 1 | 100 |
| 604 | 54 | 139 | 0 | 1 | 94 |
| 605 | 373 | 139 | 0 | 1 | 115 |
| 606 | 401 | 139 | 0 | 1 | 108 |
| 607 | 367 | 139 | 0 | 1 | 127 |
| 608 | 609 | 139 | 0 | 1 | 111 |
| 609 | 297 | 139 | 0 | 5 | 99 |
| 610 | 344 | 139 | 0 | 1 | 98 |
| 611 | 422 | 139 | 0 | 1 | 99 |
| 612 | 275 | 139 | 0 | 1 | 98 |
| 613 | 513 | 139 | 0 | 1 | 117 |
| 614 | 136 | 139 | 0 | 1 | 74 |
| 615 | 257 | 139 | 0 | 1 | 111 |
| 616 | 829 | 139 | 0 | 5 | 100 |
| 617 | 597 | 139 | 0 | 1 | 95 |
| 618 | 65 | 139 | 0 | 1 | 116 |
| 619 | 699 | 139 | 0 | 1 | 89 |
| 620 | 522 | 139 | 0 | 1 | 109 |
| 621 | 901 | 139 | 0 | 1 | 137 |
| 622 | 504 | 139 | 0 | 1 | 122 |
| 623 | 542 | 139 | 0 | 1 | 88 |
| 624 | 71 | 139 | 0 | 5 | 91 |
| 625 | 406 | 139 | 0 | 1 | 96 |
| 626 | 570 | 139 | 0 | 1 | 119 |
| 627 | 319 | 139 | 0 | 1 | 124 |
| 628 | 929 | 139 | 0 | 1 | 99 |

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|---|---|---|---|---|---|
| 629 | 109 | 139 | 0 | 1 | 94 |
| 630 | 852 | 139 | 0 | 1 | 104 |
| 631 | 159 | 139 | 0 | 1 | 101 |
| 632 | 381 | 139 | 0 | 1 | 98 |
| 633 | 354 | 139 | 0 | 1 | 121 |
| 634 | 739 | 139 | 0 | 1 | 100 |
| 635 | 310 | 139 | 0 | 1 | 133 |
| 636 | 627 | 139 | 0 | 1 | 111 |
| 637 | 322 | 139 | 0 | 5 | 88 |
| 638 | 567 | 139 | 0 | 1 | 106 |
| 639 | 351 | 139 | 0 | 1 | 92 |
| 640 | 206 | 139 | 0 | 1 | 106 |
| 641 | 870 | 139 | 0 | 1 | 114 |
| 642 | 517 | 150 | 1 | 5 | 556 |
| 643 | 581 | 150 | 0 | 5 | 144 |
| 644 | 223 | 150 | 1 | 1 | 512 |
| 645 | 538 | 150 | 0 | 5 | 175 |
| 646 | 19 | 150 | 1 | 1 | 652 |
| 647 | 258 | 150 | 0 | 1 | 172 |
| 648 | 686 | 150 | 1 | 5 | 525 |
| 649 | 492 | 150 | 0 | 1 | 157 |
| 650 | 801 | 150 | 1 | 1 | 522 |
| 651 | 815 | 150 | 0 | 1 | 172 |
| 652 | 677 | 150 | 1 | 1 | 478 |
| 653 | 23 | 150 | 0 | 2 | 171 |
| 654 | 98 | 150 | 1 | 1 | 565 |
| 655 | 613 | 150 | 1 | 2 | 517 |
| 656 | 773 | 150 | 0 | 1 | 162 |
| 657 | 704 | 150 | 1 | 5 | 595 |
| 658 | 49 | 150 | 0 | 5 | 145 |
| 659 | 924 | 150 | 0 | 1 | 164 |
| 660 | 151 | 150 | 0 | 5 | 138 |
| 661 | 900 | 150 | 0 | 1 | 142 |
| 662 | 145 | 150 | 1 | 1 | 573 |
| 663 | 445 | 150 | 0 | 2 | 130 |
| 664 | 883 | 150 | 0 | 1 | 121 |
| 665 | 140 | 150 | 1 | 1 | 558 |
| 666 | 55 | 150 | 0 | 1 | 129 |
| 667 | 507 | 150 | 1 | 5 | 483 |
| 668 | 592 | 150 | 0 | 5 | 128 |
| 669 | 303 | 150 | 1 | 5 | 499 |
| 670 | 11 | 150 | 1 | 1 | 513 |
| 671 | 240 | 150 | 0 | 5 | 130 |
| 672 | 324 | 150 | 1 | 5 | 499 |
| 673 | 211 | 150 | 0 | 1 | 170 |
| 674 | 478 | 150 | 1 | 1 | 559 |
| 675 | 933 | 150 | 1 | 1 | 487 |
| 676 | 930 | 150 | 1 | 1 | 536 |
| 677 | 321 | 150 | 1 | 1 | 550 |
| 678 | 36 | 150 | 0 | 5 | 109 |
| 679 | 743 | 150 | 1 | 1 | 516 |
| 680 | 437 | 150 | 1 | 1 | 559 |
| 681 | 279 | 150 | 1 | 1 | 587 |
| 682 | 287 | 150 | 1 | 5 | 501 |
| 683 | 537 | 150 | 0 | 5 | 154 |
| 684 | 576 | 150 | 1 | 1 | 571 |
| 685 | 668 | 150 | 0 | 5 | 121 |
| 686 | 580 | 150 | 1 | 1 | 547 |
| 687 | 783 | 150 | 1 | 1 | 517 |
| 688 | 792 | 150 | 1 | 1 | 590 |
| 689 | 50 | 150 | 0 | 5 | 169 |
| 690 | 713 | 150 | 1 | 1 | 576 |
| 691 | 608 | 150 | 0 | 5 | 112 |
| 692 | 187 | 150 | 1 | 1 | 541 |
| 693 | 268 | 150 | 0 | 5 | 143 |
| 694 | 138 | 150 | 0 | 5 | 133 |
| 695 | 779 | 150 | 0 | 5 | 138 |
| 696 | 700 | 150 | 0 | 5 | 181 |
| 697 | 572 | 150 | 1 | 1 | 606 |
| 698 | 196 | 150 | 1 | 1 | 605 |
| 699 | 212 | 150 | 0 | 1 | 163 |
| 700 | 364 | 150 | 0 | 1 | 159 |
| 701 | 560 | 150 | 1 | 1 | 529 |
| 702 | 485 | 136 | 1 | 1 | 585 |
| 703 | 553 | 136 | 1 | 1 | 515 |
| 704 | 861 | 136 | 1 | 1 | 508 |
| 705 | 764 | 136 | 0 | 1 | 158 |
| 706 | 28 | 136 | 0 | 1 | 136 |
| 707 | 229 | 136 | 1 | 1 | 543 |
| 708 | 961 | 136 | 1 | 1 | 571 |
| 709 | 444 | 136 | 1 | 1 | 627 |
| 710 | 654 | 136 | 1 | 1 | 505 |
| 711 | 379 | 136 | 1 | 1 | 617 |
| 712 | 308 | 136 | 1 | 1 | 576 |
| 713 | 564 | 136 | 1 | 1 | 538 |
| 714 | 181 | 136 | 1 | 1 | 534 |
| 715 | 810 | 136 | 1 | 2 | 592 |
| 716 | 698 | 136 | 1 | 1 | 573 |
| 717 | 169 | 136 | 1 | 1 | 603 |
| 718 | 825 | 136 | 1 | 1 | 582 |
| 719 | 611 | 136 | 1 | 1 | 506 |
| 720 | 128 | 136 | 1 | 1 | 562 |
| 721 | 496 | 136 | 1 | 1 | 582 |
| 722 | 413 | 136 | 1 | 1 | 592 |
| 723 | 117 | 136 | 1 | 1 | 559 |
| 724 | 29 | 136 | 1 | 1 | 506 |
| 725 | 656 | 136 | 1 | 3 | 564 |
| 726 | 436 | 136 | 1 | 1 | 578 |
| 727 | 738 | 136 | 1 | 1 | 601 |
| 728 | 747 | 136 | 1 | 1 | 570 |
| 729 | 697 | 143 | 0 | 1 | 132 |
| 730 | 619 | 143 | 1 | 1 | 518 |
| 731 | 763 | 143 | 0 | 1 | 140 |
| 732 | 516 | 143 | 1 | 1 | 645 |
| 733 | 867 | 143 | 1 | 1 | 646 |
| 734 | 707 | 143 | 1 | 1 | 643 |
| 735 | 949 | 143 | 0 | 1 | 193 |
| 736 | 435 | 143 | 0 | 2 | 116 |
| 737 | 398 | 143 | 1 | 1 | 631 |
| 738 | 234 | 143 | 1 | 1 | 549 |
| 739 | 508 | 143 | 1 | 1 | 661 |
| 740 | 716 | 143 | 0 | 1 | 143 |
| 741 | 818 | 143 | 1 | 1 | 538 |
| 742 | 86 | 143 | 1 | 1 | 714 |
| 743 | 119 | 143 | 1 | 1 | 554 |
| 744 | 819 | 143 | 1 | 5 | 449 |
| 745 | 208 | 143 | 1 | 1 | 626 |
| 746 | 165 | 143 | 1 | 1 | 597 |
| 747 | 944 | 140 | 0 | 1 | 106 |
| 748 | 333 | 165 | 0 | 1 | 107 |
| 749 | 709 | 165 | 0 | 5 | 133 |
| 750 | 549 | 165 | 1 | 1 | 648 |
| 751 | 414 | 165 | 1 | 5 | 704 |
| 752 | 842 | 165 | 0 | 1 | 155 |
| 753 | 711 | 165 | 0 | 2 | 146 |
| 754 | 926 | 154 | 0 | 1 | 159 |
| 755 | 568 | 154 | 0 | 1 | 160 |
| 756 | 82 | 154 | 0 | 1 | 152 |
| 757 | 891 | 154 | 0 | 1 | 164 |
| 758 | 35 | 154 | 0 | 1 | 148 |
| 759 | 579 | 154 | 0 | 1 | 159 |
| 760 | 73 | 154 | 0 | 1 | 152 |
| 761 | 662 | 154 | 0 | 1 | 156 |
| 762 | 454 | 154 | 0 | 1 | 171 |
| 763 | 163 | 153 | 0 | 6 | 112 |
| 764 | 778 | 153 | 0 | 1 | 126 |
| 765 | 376 | 153 | 0 | 5 | 126 |
| 766 | 99 | 148 | 0 | 1 | 134 |
| 767 | 407 | 148 | 0 | 2 | 142 |
| 768 | 448 | 148 | 0 | 2 | 141 |
| 769 | 798 | 148 | 0 | 1 | 169 |
| 770 | 596 | 148 | 0 | 6 | 138 |
| 771 | 338 | 148 | 0 | 1 | 197 |
| 772 | 217 | 148 | 0 | 1 | 169 |
| 773 | 550 | 148 | 0 | 2 | 151 |
| 774 | 227 | 148 | 0 | 5 | 124 |
| 775 | 665 | 148 | 0 | 1 | 141 |
| 776 | 429 | 148 | 0 | 1 | 138 |
| 777 | 24 | 148 | 0 | 1 | 163 |
| 778 | 252 | 148 | 0 | 1 | 157 |
| 779 | 701 | 148 | 0 | 6 | 101 |
| 780 | 905 | 148 | 0 | 2 | 169 |
| 781 | 31 | 148 | 0 | 2 | 106 |
| 782 | 612 | 148 | 0 | 1 | 179 |
| 783 | 124 | 148 | 0 | 2 | 110 |
| 784 | 67 | 148 | 0 | 2 | 91 |
| 785 | 511 | 148 | 1 | 2 | 638 |
| 786 | 541 | 148 | 0 | 2 | 149 |
| 787 | 909 | 148 | 0 | 2 | 121 |
| 788 | 565 | 148 | 0 | 6 | 145 |
| 789 | 293 | 148 | 1 | 2 | 636 |
| 790 | 899 | 148 | 0 | 1 | 144 |
| 791 | 483 | 148 | 0 | 2 | 148 |
| 792 | 906 | 148 | 0 | 2 | 163 |
| 793 | 131 | 148 | 0 | 1 | 128 |
| 794 | 847 | 148 | 0 | 1 | 146 |
| 795 | 710 | 148 | 0 | 2 | 141 |
| 796 | 299 | 148 | 0 | 1 | 147 |
| 797 | 149 | 148 | 0 | 1 | 140 |
| 798 | 94 | 148 | 0 | 2 | 134 |
| 799 | 442 | 148 | 0 | 2 | 152 |

| | | | | | |
|---|---|---|---|---|---|
| 800 | 340 | 148 | 0 | 2 | 171 |
| 801 | 202 | 148 | 0 | 1 | 134 |
| 802 | 48 | 148 | 0 | 1 | 179 |
| 803 | 894 | 148 | 0 | 1 | 158 |
| 804 | 918 | 148 | 0 | 1 | 172 |
| 805 | 823 | 148 | 0 | 2 | 168 |
| 806 | 369 | 148 | 0 | 1 | 147 |
| 807 | 820 | 148 | 0 | 1 | 150 |
| 808 | 418 | 148 | 0 | 6 | 130 |
| 809 | 146 | 148 | 0 | 2 | 167 |
| 810 | * | 148 | 0 | 5 | 100 |
| 811 | 277 | 148 | 0 | 2 | 161 |
| 812 | 400 | 148 | 0 | 5 | 138 |
| 813 | 410 | 148 | 0 | 2 | 150 |
| 814 | 526 | 148 | 0 | 1 | 174 |
| 815 | 77 | 148 | 0 | 1 | 175 |
| 816 | 806 | 148 | 0 | 2 | 155 |
| 817 | 790 | 148 | 0 | 6 | 167 |
| 818 | * | 148 | 0 | 1 | 171 |
| 819 | 126 | 148 | 0 | 6 | 116 |
| 820 | 13 | 148 | 0 | 2 | 142 |
| 821 | 155 | 148 | 0 | 5 | 153 |
| 822 | 683 | 148 | 0 | 6 | 128 |
| 823 | * | 145 | 1 | 7 | 523 |
| 824 | 598 | 145 | 1 | 5 | 422 |
| 825 | 461 | 145 | 1 | 5 | 454 |
| 826 | 368 | 145 | 1 | 5 | 446 |
| 827 | 399 | 145 | 1 | 5 | 447 |
| 828 | 121 | 145 | 1 | 5 | 555 |
| 829 | 484 | 145 | 1 | 1 | 623 |
| 830 | 356 | 145 | 1 | 1 | 522 |
| 831 | 26 | 145 | 0 | 1 | 185 |
| 832 | 856 | 145 | 1 | 1 | 526 |
| 833 | 105 | 145 | 1 | 1 | 483 |
| 834 | 578 | 145 | 1 | 1 | 624 |
| 835 | 524 | 145 | 1 | 1 | 571 |
| 836 | 174 | 145 | 1 | 1 | 604 |
| 837 | 189 | 145 | 1 | 5 | 575 |
| 838 | 46 | 145 | 1 | 1 | 555 |
| 839 | 334 | 145 | 1 | 1 | 566 |
| 840 | 402 | 145 | 1 | 1 | 503 |
| 841 | 167 | 145 | 1 | 5 | 544 |
| 842 | 760 | 145 | 1 | 5 | 538 |
| 843 | 47 | 145 | 1 | 1 | 516 |
| 844 | 672 | 145 | 1 | 1 | 383 |
| 845 | 317 | 145 | 1 | 1 | 533 |
| 846 | 79 | 145 | 1 | 1 | 548 |
| 847 | 959 | 145 | 1 | 1 | 547 |
| 848 | 826 | 145 | 1 | 1 | 609 |
| 849 | 745 | 145 | 1 | 1 | 625 |
| 850 | 254 | 145 | 1 | 5 | 520 |
| 851 | 342 | 145 | 1 | 1 | 577 |
| 852 | 172 | 145 | 1 | 5 | 509 |
| 853 | 964 | 145 | 1 | 6 | 533 |
| 854 | 243 | 145 | 1 | 1 | 477 |
| 855 | 766 | 145 | 1 | 3 | 480 |
| 856 | 347 | 149 | 1 | 2 | 543 |
| 857 | 38 | 149 | 0 | 1 | 131 |
| 858 | 337 | 149 | 0 | 1 | 101 |
| 859 | 871 | 149 | 0 | 1 | 118 |
| 860 | 781 | 149 | 0 | 5 | 92 |
| 861 | 388 | 149 | 1 | 1 | 575 |
| 862 | 644 | 149 | 0 | 1 | 81 |
| 863 | 594 | 149 | 1 | 1 | 637 |
| 864 | 120 | 149 | 0 | 5 | 90 |
| 865 | 396 | 149 | 1 | 5 | 438 |
| 866 | 850 | 149 | 0 | 1 | 145 |
| 867 | 100 | 149 | 0 | 1 | 95 |
| 868 | 667 | 149 | 0 | 1 | 99 |
| 869 | 307 | 149 | 0 | 1 | 100 |
| 870 | 563 | 149 | 0 | 1 | 129 |
| 871 | 915 | 149 | 1 | 1 | 635 |
| 872 | 531 | 149 | 1 | 1 | 605 |
| 873 | 190 | 149 | 0 | 1 | 136 |
| 874 | 129 | 149 | 0 | 1 | 136 |
| 875 | 452 | 149 | 0 | 1 | 145 |
| 876 | 726 | 149 | 0 | 3 | 75 |
| 877 | 391 | 149 | 0 | 1 | 135 |
| 878 | 659 | 149 | 0 | 1 | 111 |
| 879 | 922 | 149 | 1 | 1 | 633 |
| 880 | 153 | 149 | 0 | 1 | 91 |
| 881 | 224 | 149 | 0 | 1 | 93 |
| 882 | 749 | 149 | 0 | 1 | 107 |
| 883 | 618 | 149 | 0 | 1 | 118 |
| 884 | 554 | 149 | 0 | 1 | 100 |
| 885 | 315 | 149 | 0 | 1 | 129 |
| 886 | 523 | 149 | 0 | 1 | 113 |
| 887 | 301 | 149 | 1 | 5 | 457 |
| 888 | 395 | 149 | 0 | 5 | 92 |
| 889 | 201 | 149 | 0 | 1 | 114 |
| 890 | 962 | 149 | 0 | 2 | 78 |
| 891 | 886 | 149 | 0 | 2 | 102 |
| 892 | 425 | 149 | 0 | 1 | 149 |
| 893 | 908 | 149 | 0 | 1 | 99 |
| 894 | 963 | 149 | 0 | 1 | 105 |
| 895 | 198 | 149 | 0 | 1 | 92 |
| 896 | 420 | 149 | 0 | 2 | 102 |
| 897 | 248 | 149 | 0 | 2 | 93 |
| 898 | 628 | 149 | 0 | 1 | 150 |
| 899 | 205 | 149 | 0 | 1 | 84 |
| 900 | 423 | 149 | 0 | 1 | 89 |
| 901 | 61 | 149 | 0 | 1 | 105 |
| 902 | 348 | 149 | 0 | 1 | 133 |
| 903 | 722 | 149 | 0 | 1 | 104 |
| 904 | 21 | 149 | 1 | 1 | 623 |
| 905 | 241 | 149 | 0 | 1 | 101 |
| 906 | 904 | 149 | 0 | 2 | 76 |
| 907 | 173 | 149 | 1 | 1 | 669 |
| 908 | 247 | 149 | 0 | 1 | 122 |
| 909 | 805 | 149 | 0 | 1 | 133 |
| 910 | 731 | 149 | 0 | 6 | 98 |
| 911 | 214 | 149 | 1 | 1 | 625 |
| 912 | 813 | 149 | 0 | 2 | 80 |
| 913 | 451 | 149 | 0 | 1 | 87 |
| 914 | 231 | 164 | 1 | 3 | 569 |
| 915 | 266 | 164 | 1 | 1 | 541 |
| 916 | 359 | 164 | 1 | 1 | 585 |
| 917 | 718 | 164 | 0 | 1 | 155 |
| 918 | 260 | 146 | 0 | 1 | 172 |
| 919 | 130 | 146 | 0 | 1 | 159 |
| 920 | 884 | 146 | 0 | 1 | 144 |
| 921 | 650 | 146 | 0 | 5 | 127 |
| 922 | 468 | 146 | 1 | 2 | 538 |
| 923 | 298 | 146 | 1 | 1 | 634 |
| 924 | 114 | 146 | 1 | 1 | 588 |
| 925 | 940 | 146 | 0 | 1 | 157 |
| 926 | 328 | 146 | 0 | 1 | 150 |
| 927 | 200 | 146 | 1 | 1 | 568 |
| 928 | 83 | 146 | 0 | 1 | 161 |
| 929 | 288 | 146 | 0 | 1 | 154 |
| 930 | 878 | 146 | 1 | 1 | 635 |
| 931 | 518 | 146 | 1 | 1 | 658 |
| 932 | * | 146 | 1 | 1 | 630 |
| 933 | 123 | 146 | 0 | 1 | 161 |
| 934 | 60 | 146 | 0 | 1 | 125 |
| 935 | 135 | 146 | 0 | 1 | 134 |
| 936 | 377 | 146 | 1 | 1 | 523 |
| 937 | 197 | 146 | 0 | 1 | 143 |
| 938 | 237 | 146 | 1 | 1 | 651 |
| 939 | 264 | 146 | 1 | 1 | 546 |
| 940 | 547 | 146 | 1 | 1 | 666 |
| 941 | 660 | 146 | 1 | 6 | 522 |
| 942 | 692 | 146 | 1 | 1 | 637 |
| 943 | 417 | 146 | 0 | 1 | 148 |
| 944 | 885 | 146 | 1 | 5 | 630 |
| 945 | 877 | 146 | 1 | 1 | 641 |
| 946 | 41 | 146 | 0 | 5 | 149 |
| 947 | 69 | 146 | 0 | 1 | 158 |
| 948 | 497 | 146 | 1 | 1 | 606 |
| 949 | 183 | 146 | 1 | 1 | 651 |
| 950 | 626 | 146 | 0 | 1 | 180 |
| 951 | 706 | 146 | 1 | 1 | 623 |
| 952 | 476 | 146 | 1 | 3 | 692 |
| 953 | 506 | 146 | 1 | 1 | 642 |
| 954 | 385 | 146 | 0 | 1 | 136 |
| 955 | 811 | 146 | 0 | 1 | 181 |
| 956 | 630 | 146 | 0 | 1 | 125 |
| 957 | 481 | 146 | 0 | 1 | 131 |
| 958 | 342 | 146 | 0 | 1 | 172 |
| 959 | 787 | 146 | 1 | 1 | 596 |
| 960 | 646 | 146 | 0 | 1 | 134 |
| 961 | 807 | 146 | 0 | 1 | 132 |
| 962 | 244 | 146 | 0 | 1 | 160 |
| 963 | 832 | 146 | 0 | 1 | 128 |
| 964 | 688 | 146 | 0 | 1 | 113 |
| 965 | 312 | 146 | 1 | 1 | 625 |
| 966 | 118 | 146 | 1 | 1 | 548 |
| 967 | 141 | 146 | 1 | 1 | 629 |
| 968 | 162 | 146 | 0 | 1 | 143 |
| 969 | 195 | 146 | 1 | 1 | 628 |
| 970 | 742 | 146 | 0 | 1 | 141 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 971 | 872 | 146 | 0 | 1 | 155 | 973 | 271 | 146 | 0 | 1 | 153 |
| 972 | 675 | 146 | 1 | 1 | 533 | 974 | 233 | 146 | 0 | 1 | 140 |

The data for batch #2 are shown below. This time no TUB numbers were duplicated or omitted, and, of the ORD numbers, only two were duplicated (74 and 179) and one omitted (279). Since the maximum ORD value was 687, then the actual number of sexuals weighed was (687 + 2 - 1) = 688, as required. Table A3.3 above shows which TUB numbers refer to which sexuals.

| TUB | ORD | COL | SX | CN | DW | 36 | 656 | 169 | 0 | 2 | 197 | 73 | 386 | 184 | 1 | 5 | 552 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 37 | 324 | 169 | 1 | 1 | 639 | 74 | 117 | 184 | 1 | 2 | 573 |
| 1 | 147 | 186 | 1 | 1 | 610 | 38 | 208 | 169 | 0 | 1 | 159 | 75 | 454 | 184 | 0 | 1 | 185 |
| 2 | 650 | 186 | 1 | 1 | 657 | 39 | 376 | 169 | 0 | 1 | 162 | 76 | 373 | 184 | 1 | 1 | 553 |
| 3 | 47 | 186 | 1 | 1 | 684 | 40 | 629 | 169 | 0 | 1 | 171 | 77 | 580 | 184 | 1 | 1 | 555 |
| 4 | 371 | 186 | 1 | 1 | 637 | 41 | 429 | 172 | 0 | 1 | 156 | 78 | 654 | 184 | 1 | 1 | 688 |
| 5 | 589 | 186 | 1 | 1 | 593 | 42 | 573 | 172 | 0 | 1 | 172 | 79 | 77 | 184 | 1 | 1 | 712 |
| 6 | 343 | 186 | 0 | 1 | 201 | 43 | 59 | 172 | 0 | 1 | 154 | 80 | 442 | 184 | 1 | 1 | 645 |
| 7 | 43 | 186 | 1 | 1 | 588 | 44 | 670 | 172 | 0 | 1 | 134 | 81 | 128 | 184 | 0 | 1 | 155 |
| 8 | 176 | 186 | 1 | 1 | 678 | 45 | 686 | 172 | 0 | 1 | 181 | 82 | 203 | 184 | 1 | 1 | 688 |
| 9 | 642 | 186 | 1 | 1 | 615 | 46 | 553 | 193 | 0 | 1 | 218 | 83 | 395 | 184 | 1 | 1 | 585 |
| 10 | 202 | 186 | 1 | 1 | 724 | 47 | 491 | 193 | 0 | 1 | 162 | 84 | 310 | 184 | 1 | 2 | 633 |
| 11 | 390 | 186 | 1 | 1 | 692 | 48 | 375 | 193 | 0 | 1 | 242 | 85 | 97 | 184 | 0 | 1 | 189 |
| 12 | 219 | 186 | 1 | 1 | 586 | 49 | 606 | 193 | 0 | 1 | 187 | 86 | 363 | 184 | 1 | 1 | 578 |
| 13 | 554 | 186 | 1 | 1 | 556 | 50 | 664 | 193 | 0 | 1 | 202 | 87 | 441 | 184 | 1 | 1 | 515 |
| 14 | 653 | 186 | 1 | 1 | 678 | 51 | 248 | 193 | 0 | 1 | 203 | 88 | 335 | 184 | 1 | 1 | 532 |
| 15 | 81 | 186 | 1 | 1 | 640 | 52 | 538 | 193 | 0 | 1 | 190 | 89 | 182 | 184 | 1 | 1 | 625 |
| 16 | 475 | 186 | 1 | 1 | 598 | 53 | 604 | 193 | 0 | 1 | 191 | 90 | 205 | 184 | 1 | 5 | 719 |
| 17 | 99 | 186 | 1 | 1 | 684 | 54 | 366 | 193 | 0 | 1 | 198 | 91 | 16 | 184 | 1 | 1 | 654 |
| 18 | 473 | 186 | 1 | 1 | 641 | 55 | 311 | 193 | 0 | 1 | 179 | 92 | 461 | 184 | 1 | 1 | 610 |
| 19 | 52 | 186 | 1 | 1 | 682 | 56 | 528 | 193 | 0 | 1 | 193 | 93 | 179 | 184 | 1 | 1 | 648 |
| 20 | 531 | 186 | 1 | 1 | 692 | 57 | 273 | 193 | 1 | 2 | 531 | 94 | 238 | 184 | 1 | 1 | 566 |
| 21 | 190 | 186 | 1 | 1 | 675 | 58 | 677 | 193 | 0 | 1 | 184 | 95 | 179 | 184 | 1 | 1 | 555 |
| 22 | 384 | 186 | 1 | 1 | 671 | 59 | 13 | 193 | 0 | 1 | 197 | 96 | 286 | 184 | 1 | 3 | 557 |
| 23 | 31 | 186 | 1 | 1 | 609 | 60 | 29 | 193 | 0 | 1 | 205 | 97 | 613 | 184 | 1 | 2 | 683 |
| 24 | 663 | 186 | 1 | 1 | 546 | 61 | 149 | 193 | 0 | 1 | 192 | 98 | 493 | 184 | 1 | 1 | 637 |
| 25 | 104 | 186 | 1 | 1 | 683 | 62 | 289 | 171 | 1 | 5 | 604 | 99 | 583 | 184 | 1 | 1 | 644 |
| 26 | 566 | 186 | 1 | 1 | 647 | 63 | 305 | 171 | 1 | 1 | 651 | 100 | 332 | 184 | 0 | 1 | 161 |
| 27 | 86 | 186 | 0 | 1 | 162 | 64 | 300 | 171 | 1 | 1 | 674 | 101 | 192 | 184 | 0 | 1 | 167 |
| 28 | 444 | 186 | 1 | 1 | 760 | 65 | 22 | 171 | 1 | 1 | 682 | 102 | 502 | 184 | 1 | 5 | 535 |
| 29 | 394 | 186 | 1 | 1 | 632 | 66 | 252 | 171 | 1 | 1 | 685 | 103 | 194 | 184 | 1 | 1 | 616 |
| 30 | 616 | 186 | 1 | 1 | 648 | 67 | 61 | 171 | 1 | 1 | 667 | 104 | 235 | 184 | 1 | 1 | 599 |
| 31 | 571 | 186 | 1 | 1 | 662 | 68 | 447 | 189 | 0 | 1 | 141 | 105 | 116 | 184 | 1 | 1 | 777 |
| 32 | 74 | 186 | 1 | 1 | 561 | 69 | 399 | 194 | 0 | 1 | 185 | 106 | 529 | 184 | 1 | 1 | 677 |
| 33 | 60 | 186 | 1 | 1 | 640 | 70 | 141 | 194 | 0 | 1 | 135 | 107 | 21 | 184 | 1 | 1 | 623 |
| 34 | 66 | 186 | 1 | 1 | 617 | 71 | 542 | 194 | 0 | 1 | 181 | 108 | 102 | 184 | 1 | 1 | 659 |
| 35 | 494 | 186 | 1 | 1 | 605 | 72 | 118 | 184 | 0 | 1 | 152 | 109 | 361 | 184 | 0 | 1 | 147 |

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|---|---|---|---|---|---|
| 110 | 293 | 184 | 1 | 1 | 663 |
| 111 | 159 | 184 | 1 | 1 | 596 |
| 112 | 165 | 184 | 1 | 1 | 557 |
| 113 | 228 | 184 | 1 | 1 | 622 |
| 114 | 636 | 184 | 1 | 2 | 603 |
| 115 | 269 | 184 | 1 | 1 | 590 |
| 116 | 687 | 184 | 1 | 1 | 677 |
| 117 | 345 | 184 | 1 | 1 | 563 |
| 118 | 222 | 184 | 1 | 1 | 628 |
| 119 | 9 | 184 | 1 | 1 | 717 |
| 120 | 565 | 184 | 1 | 1 | 607 |
| 121 | 452 | 184 | 1 | 1 | 693 |
| 122 | 71 | 184 | 1 | 1 | 708 |
| 123 | 250 | 184 | 0 | 1 | 154 |
| 124 | 601 | 184 | 0 | 1 | 148 |
| 125 | 49 | 184 | 1 | 1 | 711 |
| 126 | 389 | 184 | 1 | 1 | 583 |
| 127 | 499 | 184 | 1 | 2 | 644 |
| 128 | 660 | 184 | 1 | 7 | 554 |
| 129 | 73 | 184 | 1 | 1 | 713 |
| 130 | 307 | 184 | 1 | 1 | 593 |
| 131 | 600 | 184 | 1 | 2 | 520 |
| 132 | 133 | 184 | 1 | 1 | 604 |
| 133 | 145 | 184 | 1 | 1 | 639 |
| 134 | 587 | 184 | 1 | 1 | 708 |
| 135 | 365 | 184 | 0 | 1 | 163 |
| 136 | 291 | 184 | 1 | 1 | 566 |
| 137 | 669 | 184 | 1 | 2 | 580 |
| 138 | 35 | 184 | 0 | 1 | 154 |
| 139 | 234 | 173 | 0 | 1 | 120 |
| 140 | 408 | 173 | 0 | 1 | 133 |
| 141 | 351 | 173 | 0 | 1 | 140 |
| 142 | 505 | 173 | 0 | 1 | 120 |
| 143 | 189 | 173 | 0 | 1 | 120 |
| 144 | 388 | 173 | 0 | 1 | 114 |
| 145 | 585 | 173 | 0 | 6 | 117 |
| 146 | 615 | 173 | 0 | 1 | 114 |
| 147 | 534 | 173 | 0 | 1 | 142 |
| 148 | 44 | 173 | 0 | 1 | 124 |
| 149 | 185 | 173 | 0 | 1 | 118 |
| 150 | 258 | 173 | 0 | 1 | 120 |
| 151 | 631 | 173 | 0 | 1 | 112 |
| 152 | 221 | 173 | 0 | 1 | 110 |
| 153 | 625 | 173 | 0 | 1 | 144 |
| 154 | 112 | 173 | 0 | 1 | 110 |
| 155 | 41 | 173 | 0 | 1 | 119 |
| 156 | 508 | 173 | 0 | 1 | 127 |
| 157 | 557 | 173 | 0 | 1 | 134 |
| 158 | 137 | 173 | 0 | 1 | 140 |
| 159 | 82 | 173 | 0 | 1 | 112 |
| 160 | 413 | 173 | 0 | 1 | 129 |
| 161 | 199 | 173 | 0 | 1 | 164 |
| 162 | 422 | 173 | 0 | 1 | 130 |
| 163 | 523 | 173 | 0 | 1 | 131 |
| 164 | 6 | 173 | 0 | 1 | 128 |
| 165 | 251 | 173 | 0 | 1 | 112 |
| 166 | 48 | 173 | 0 | 1 | 126 |
| 167 | 683 | 173 | 0 | 1 | 95 |
| 168 | 319 | 173 | 0 | 1 | 134 |
| 169 | 245 | 191 | 1 | 1 | 721 |
| 170 | 374 | 191 | 1 | 1 | 737 |
| 171 | 500 | 191 | 1 | 1 | 718 |
| 172 | 93 | 191 | 1 | 5 | 578 |
| 173 | 532 | 191 | 0 | 2 | 106 |
| 174 | 151 | 191 | 0 | 1 | 147 |
| 175 | 247 | 191 | 0 | 1 | 189 |
| 176 | 484 | 191 | 0 | 2 | 105 |
| 177 | 635 | 191 | 1 | 1 | 735 |
| 178 | 501 | 191 | 1 | 1 | 686 |
| 179 | 419 | 191 | 0 | 1 | 161 |
| 180 | 652 | 191 | 1 | 1 | 728 |
| 181 | 393 | 191 | 1 | 1 | 710 |
| 182 | 456 | 191 | 0 | 1 | 131 |
| 183 | 156 | 191 | 1 | 1 | 738 |
| 184 | 593 | 191 | 1 | 2 | 659 |
| 185 | 98 | 191 | 0 | 2 | 98 |
| 186 | 126 | 191 | 1 | 1 | 769 |
| 187 | 100 | 191 | 1 | 1 | 710 |
| 188 | 257 | 191 | 1 | 1 | 759 |
| 189 | 570 | 191 | 0 | 2 | 102 |
| 190 | 297 | 191 | 1 | 1 | 638 |
| 191 | 379 | 192 | 1 | 1 | 676 |
| 192 | 23 | 192 | 1 | 1 | 645 |
| 193 | 172 | 192 | 1 | 1 | 693 |
| 194 | 131 | 192 | 1 | 1 | 698 |
| 195 | 385 | 192 | 1 | 1 | 660 |
| 196 | 197 | 192 | 1 | 1 | 660 |
| 197 | 226 | 192 | 1 | 1 | 577 |
| 198 | 19 | 182 | 0 | 1 | 132 |
| 199 | 572 | 182 | 0 | 1 | 148 |
| 200 | 183 | 182 | 0 | 1 | 150 |
| 201 | 209 | 182 | 0 | 1 | 197 |
| 202 | 440 | 182 | 0 | 1 | 177 |
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| 205 | 233 | 175 | 1 | 1 | 613 |
| 206 | 370 | 175 | 1 | 5 | 680 |
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| 208 | 647 | 190 | 0 | 1 | 121 |
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| 210 | 668 | 181 | 1 | 1 | 695 |
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| 214 | 492 | 181 | 1 | 1 | 700 |
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| 221 | 614 | 195 | 1 | 2 | 607 |
| 222 | 518 | 195 | 0 | 1 | 164 |
| 223 | 674 | 195 | 1 | 6 | 305 |
| 224 | 378 | 195 | 1 | 1 | 614 |
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| 227 | 12 | 195 | 0 | 1 | 198 |
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| 254 | 322 | 177 | 0 | 1 | 165 |
| 255 | 398 | 177 | 0 | 1 | 147 |
| 256 | 135 | 177 | 0 | 1 | 129 |
| 257 | 167 | 177 | 0 | 1 | 158 |
| 258 | 558 | 177 | 0 | 1 | 139 |
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| 260 | 106 | 177 | 0 | 1 | 173 |
| 261 | 434 | 177 | 0 | 1 | 146 |
| 262 | 283 | 188 | 1 | 1 | 607 |
| 263 | 451 | 183 | 0 | 1 | 110 |
| 264 | 87 | 183 | 0 | 1 | 126 |
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| 267 | 154 | 183 | 0 | 1 | 130 |
| 268 | 198 | 183 | 0 | 1 | 145 |
| 269 | 560 | 183 | 0 | 1 | 131 |
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| 271 | 681 | 183 | 0 | 1 | 121 |
| 272 | 288 | 183 | 0 | 1 | 142 |
| 273 | 355 | 183 | 0 | 1 | 118 |
| 274 | 152 | 183 | 0 | 1 | 125 |
| 275 | 303 | 183 | 0 | 1 | 142 |
| 276 | 236 | 183 | 0 | 1 | 152 |
| 277 | 415 | 183 | 0 | 1 | 109 |
| 278 | 55 | 183 | 0 | 1 | 151 |
| 279 | 287 | 183 | 0 | 1 | 132 |
| 280 | 490 | 183 | 0 | 1 | 120 |

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| 281 | 464 | 183 | 0 | 1 | 100 |
| 282 | 511 | 183 | 0 | 1 | 63 |
| 283 | 315 | 183 | 0 | 1 | 119 |
| 284 | 105 | 183 | 0 | 1 | 131 |
| 285 | 333 | 183 | 0 | 1 | 175 |
| 286 | 119 | 183 | 0 | 1 | 140 |
| 287 | 50 | 183 | 0 | 1 | 119 |
| 288 | 564 | 183 | 0 | 1 | 133 |
| 289 | 89 | 183 | 0 | 1 | 138 |
| 290 | 274 | 183 | 0 | 1 | 120 |
| 291 | 424 | 178 | 0 | 1 | 170 |
| 292 | 120 | 178 | 0 | 2 | 169 |
| 293 | 671 | 178 | 0 | 1 | 169 |
| 294 | 309 | 178 | 0 | 1 | 170 |
| 295 | 263 | 178 | 0 | 1 | 172 |
| 296 | 254 | 178 | 0 | 1 | 114 |
| 297 | 96 | 185 | 0 | 1 | 143 |
| 298 | 174 | 185 | 1 | 1 | 678 |
| 299 | 177 | 185 | 1 | 1 | 632 |
| 300 | 253 | 185 | 1 | 1 | 614 |
| 301 | 175 | 185 | 1 | 1 | 632 |
| 302 | 83 | 167 | 1 | 1 | 782 |
| 303 | 56 | 167 | 1 | 1 | 743 |
| 304 | 282 | 167 | 0 | 5 | 165 |
| 305 | 655 | 167 | 1 | 1 | 665 |
| 306 | 249 | 167 | 1 | 1 | 646 |
| 307 | 191 | 167 | 1 | 1 | 726 |
| 308 | 218 | 167 | 0 | 1 | 164 |
| 309 | 552 | 167 | 1 | 1 | 741 |
| 310 | 621 | 167 | 1 | 6 | 656 |
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| 314 | 459 | 170 | 0 | 1 | 137 |
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| 316 | 567 | 193 | 1 | 1 | 425 |
| 317 | 496 | 172 | 0 | 1 | 99 |
| 318 | 617 | 184 | 1 | 1 | 740 |
| 319 | 524 | 184 | 1 | 1 | 568 |
| 320 | 562 | 184 | 1 | 2 | 660 |
| 321 | 468 | 184 | 1 | 1 | 656 |
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| 327 | 352 | 173 | 0 | 2 | 118 |
| 328 | 525 | 173 | 0 | 1 | 117 |
| 329 | 1 | 173 | 0 | 1 | 115 |
| 330 | 578 | 173 | 0 | 1 | 110 |
| 331 | 2 | 170 | 0 | 1 | 129 |
| 332 | 38 | 217 | 1 | 1 | 686 |
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| 334 | 178 | 217 | 1 | 1 | 667 |
| 335 | 181 | 217 | 0 | 1 | 188 |
| 336 | 426 | 217 | 0 | 1 | 175 |
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| 338 | 78 | 217 | 0 | 1 | 218 |
| 339 | 498 | 217 | 0 | 1 | 114 |
| 340 | 556 | 217 | 0 | 1 | 225 |
| 341 | 609 | 217 | 0 | 1 | 117 |
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| 344 | 240 | 217 | 0 | 1 | 222 |
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| 384 | 138 | 221 | 0 | 1 | 114 |
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| 386 | 302 | 221 | 1 | 1 | 680 |
| 387 | 640 | 221 | 0 | 1 | 115 |
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| 390 | 200 | 213 | 0 | 1 | 212 |
| 391 | 462 | 213 | 0 | 1 | 209 |
| 392 | 403 | 213 | 0 | 1 | 201 |
| 393 | 237 | 213 | 0 | 1 | 198 |
| 394 | 381 | 213 | 0 | 1 | 216 |
| 395 | 308 | 213 | 0 | 1 | 193 |
| 396 | 212 | 213 | 0 | 1 | 208 |
| 397 | 290 | 213 | 0 | 1 | 200 |
| 398 | 535 | 213 | 0 | 1 | 218 |
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| 400 | 36 | 214 | 1 | 1 | 745 |
| 401 | 533 | 214 | 1 | 1 | 723 |
| 402 | 163 | 214 | 1 | 1 | 771 |
| 403 | 559 | 214 | 1 | 1 | 769 |
| 404 | 331 | 214 | 1 | 1 | 757 |
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| 407 | 598 | 214 | 1 | 1 | 809 |
| 408 | 155 | 214 | 1 | 1 | 815 |
| 409 | 339 | 214 | 1 | 1 | 777 |
| 410 | 478 | 214 | 1 | 1 | 773 |
| 411 | 193 | 214 | 1 | 1 | 738 |
| 412 | 396 | 214 | 1 | 1 | 812 |
| 413 | 18 | 214 | 1 | 1 | 730 |
| 414 | 354 | 214 | 1 | 1 | 752 |
| 415 | 69 | 214 | 1 | 1 | 834 |
| 416 | 449 | 214 | 1 | 1 | 765 |
| 417 | 446 | 214 | 1 | 1 | 739 |
| 418 | 342 | 214 | 1 | 1 | 808 |
| 419 | 526 | 214 | 1 | 1 | 699 |
| 420 | 265 | 214 | 1 | 1 | 688 |
| 421 | 349 | 214 | 1 | 1 | 732 |
| 422 | 481 | 214 | 1 | 1 | 777 |
| 423 | 103 | 214 | 1 | 1 | 718 |
| 424 | 662 | 207 | 1 | 1 | 836 |
| 425 | 431 | 207 | 1 | 1 | 689 |
| 426 | 436 | 207 | 0 | 1 | 185 |
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| 428 | 665 | 207 | 1 | 1 | 759 |
| 429 | 314 | 207 | 1 | 1 | 600 |
| 430 | 10 | 205 | 0 | 1 | 157 |
| 431 | 466 | 205 | 0 | 2 | 171 |
| 432 | 57 | 220 | 0 | 1 | 205 |
| 433 | 162 | 220 | 1 | 1 | 789 |
| 434 | 101 | 220 | 1 | 5 | 606 |
| 435 | 420 | 220 | 1 | 1 | 665 |
| 436 | 278 | 220 | 1 | 1 | 639 |
| 437 | 150 | 220 | 1 | 1 | 631 |
| 438 | 359 | 220 | 1 | 1 | 698 |
| 439 | 347 | 220 | 1 | 1 | 669 |
| 440 | 108 | 220 | 1 | 1 | 786 |
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| 442 | 299 | 220 | 1 | 1 | 570 |
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| 444 | 323 | 220 | 1 | 1 | 769 |
| 445 | 657 | 220 | 1 | 1 | 623 |
| 446 | 187 | 220 | 1 | 1 | 672 |
| 447 | 486 | 223 | 0 | 5 | 113 |
| 448 | 285 | 223 | 0 | 1 | 166 |
| 449 | 540 | 223 | 0 | 1 | 209 |
| 450 | 329 | 223 | 0 | 1 | 195 |
| 451 | 595 | 223 | 0 | 1 | 160 |

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| 459 | 92 | 223 | 0 | 1 | 211 | 516 | 575 | 215 | 0 | 1 | 173 | 573 | 380 | 222 | 0 | 1 | 179 |
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| 461 | 421 | 223 | 0 | 1 | 185 | 518 | 109 | 215 | 0 | 1 | 189 | 575 | 216 | 199 | 0 | 1 | 143 |
| 462 | 673 | 223 | 0 | 1 | 181 | 519 | 348 | 215 | 0 | 1 | 157 | 576 | 217 | 199 | 0 | 1 | 189 |
| 463 | 45 | 196 | 1 | 1 | 706 | 520 | 15 | 215 | 0 | 1 | 176 | 577 | 215 | 199 | 0 | 1 | 153 |
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| 466 | 25 | 196 | 0 | 1 | 156 | 523 | 214 | 215 | 0 | 1 | 160 | 580 | 312 | 199 | 0 | 1 | 198 |
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| 468 | 161 | 196 | 0 | 1 | 163 | 525 | 467 | 215 | 0 | 1 | 192 | 582 | 294 | 216 | 0 | 5 | 135 |
| 469 | 326 | 196 | 0 | 1 | 157 | 526 | 94 | 215 | 0 | 1 | 161 | 583 | 264 | 216 | 0 | 1 | 168 |
| 470 | 435 | 196 | 0 | 1 | 162 | 527 | 409 | 215 | 0 | 1 | 182 | 584 | 272 | 216 | 0 | 1 | 162 |
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| 472 | 37 | 196 | 0 | 1 | 196 | 529 | 438 | 215 | 0 | 1 | 209 | 586 | 95 | 216 | 0 | 1 | 156 |
| 473 | 591 | 196 | 0 | 1 | 175 | 530 | 113 | 215 | 0 | 1 | 194 | 587 | 648 | 216 | 0 | 1 | 175 |
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| 480 | 223 | 210 | 1 | 1 | 691 | 537 | 626 | 215 | 0 | 1 | 174 | 594 | 142 | 216 | 1 | 1 | 849 |
| 481 | 39 | 210 | 1 | 1 | 768 | 538 | 555 | 215 | 0 | 1 | 166 | 595 | 24 | 216 | 1 | 1 | 764 |
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| 485 | 327 | 210 | 1 | 2 | 669 | 542 | 453 | 215 | 0 | 1 | 184 | 599 | 675 | 216 | 0 | 1 | 167 |
| 486 | 369 | 210 | 1 | 1 | 581 | 543 | 153 | 215 | 0 | 1 | 195 | 600 | 26 | 216 | 0 | 1 | 178 |
| 487 | 110 | 210 | 0 | 1 | 177 | 544 | 8 | 215 | 0 | 1 | 196 | 601 | 569 | 216 | 1 | 5 | 791 |
| 488 | 360 | 210 | 0 | 1 | 179 | 545 | 678 | 215 | 0 | 1 | 169 | 602 | 543 | 216 | 1 | 1 | 725 |
| 489 | 521 | 210 | 1 | 2 | 725 | 546 | 430 | 215 | 0 | 1 | 181 | 603 | 470 | 216 | 1 | 1 | 780 |
| 490 | 455 | 218 | 0 | 1 | 186 | 547 | 33 | 215 | 0 | 1 | 207 | 604 | 262 | 216 | 0 | 1 | 178 |
| 491 | 406 | 215 | 0 | 1 | 167 | 548 | 207 | 215 | 0 | 1 | 177 | 605 | 353 | 216 | 0 | 1 | 181 |
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| 500 | 488 | 215 | 0 | 1 | 199 | 557 | 549 | 215 | 0 | 1 | 182 | 614 | 514 | 216 | 1 | 5 | 790 |
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| 623 | 224 | 216 | 1 | 1 | 804 |
| 624 | 80 | 216 | 1 | 1 | 806 |
| 625 | 495 | 216 | 0 | 1 | 171 |
| 626 | 129 | 216 | 0 | 1 | 173 |
| 627 | 672 | 216 | 0 | 1 | 183 |
| 628 | 685 | 216 | 1 | 1 | 740 |
| 629 | 67 | 216 | 1 | 1 | 791 |
| 630 | 139 | 216 | 0 | 1 | 185 |
| 631 | 338 | 216 | 0 | 1 | 161 |
| 632 | 168 | 216 | 0 | 1 | 190 |
| 633 | 391 | 216 | 1 | 1 | 859 |
| 634 | 62 | 216 | 1 | 1 | 850 |
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| 637 | 581 | 216 | 0 | 3 | 178 |
| 638 | 667 | 216 | 0 | 1 | 193 |
| 639 | 649 | 216 | 1 | 1 | 751 |
| 640 | 659 | 216 | 0 | 1 | 122 |
| 641 | 512 | 216 | 1 | 1 | 803 |
| 642 | 64 | 216 | 0 | 1 | 164 |
| 643 | 485 | 216 | 1 | 1 | 872 |
| 644 | 471 | 216 | 0 | 1 | 159 |
| 645 | 90 | 216 | 0 | 1 | 182 |
| 646 | 341 | 216 | 1 | 1 | 829 |
| 647 | 304 | 216 | 1 | 1 | 717 |
| 648 | 220 | 201 | 0 | 1 | 137 |
| 649 | 410 | 211 | 1 | 5 | 840 |
| 650 | 472 | 211 | 1 | 1 | 811 |
| 651 | 520 | 211 | 1 | 1 | 852 |
| 652 | 301 | 211 | 0 | 1 | 194 |
| 653 | 536 | 211 | 1 | 5 | 681 |
| 654 | 638 | 203 | 1 | 1 | 710 |
| 655 | 362 | 203 | 1 | 1 | 711 |
| 656 | 551 | 203 | 1 | 1 | 699 |
| 657 | 682 | 198 | 1 | 5 | 573 |
| 658 | 144 | 217 | 1 | 2 | 720 |
| 659 | 633 | 217 | 1 | 1 | 779 |
| 660 | 121 | 210 | 1 | 2 | 560 |
| 661 | 7 | 210 | 1 | 5 | 466 |
| 662 | 266 | 210 | 1 | 5 | 655 |
| 663 | 20 | 210 | 1 | 5 | 670 |
| 664 | 70 | 210 | 1 | 1 | 710 |
| 665 | 428 | 210 | 1 | 6 | 501 |
| 666 | 608 | 210 | 1 | 2 | 524 |
| 667 | 320 | 210 | 1 | 5 | 612 |
| 668 | 605 | 210 | 1 | 6 | 778 |
| 669 | 509 | 210 | 1 | 5 | 614 |
| 670 | 644 | 210 | 1 | 2 | 693 |
| 671 | 337 | 210 | 1 | 1 | 617 |
| 672 | 32 | 210 | 1 | 5 | 585 |
| 673 | 418 | 210 | 1 | 5 | 745 |
| 674 | 125 | 210 | 1 | 1 | 715 |
| 675 | 465 | 210 | 1 | 1 | 709 |
| 676 | 603 | 210 | 1 | 5 | 720 |
| 677 | 270 | 210 | 1 | 1 | 697 |
| 678 | 68 | 210 | 1 | 2 | 710 |
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| 684 | 157 | 210 | 1 | 6 | 684 |
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| 686 | 124 | 285 | 1 | 1 | 574 |
| 687 | 284 | 263 | 0 | 2 | 213 |
| 688 | 364 | 293 | 1 | 5 | 442 |

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